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A contribution to the knowledge of the genus *Thyreus* Panzer in the West and Central Palaearctic (Hymenoptera, Apidae), with two new species, taxonomic updates, host relationships, and a key to European species

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Abstract

Thyreus Panzer, 1806, is a moderately sized bee genus containing about 115 species with an Old World distribution matching that of their principal hosts, bees of the genus *Amegilla* Friese, 1897. The Palaearctic fauna was revised during the mid-20th century but has received relatively little attention since then. New collections, examination of museum specimens, and DNA barcoding have improved our understanding of this genus in the West and Central Palaearctic. The previously unknown sexes of *T. parthenope* Lieftinck, 1968, *T. picaron* Lieftinck, 1968, and *T. priesneri* Lieftinck, 1968, are identified and clarified. New host data are presented for *Thyreus hellenicus* Lieftinck, 1968, in Greece, where it parasitises *Anthophora* (*Paramegilla*) *superans* Walker, 1871 = *Anthophora* (*Paramegilla*) *inclyta* Walker, 1871 **syn. nov.** (= *Anthophora dubia* Eversmann, 1852 sensu auctorum). A lectotype is designated for *Thyreus truncatus* (Pérez, 1884), and its range and status are discussed. New records are presented to resolve the distributional ranges of confused or poorly studied species, along with new host data. *Thyreus praevalens* (Kohl, 1905) is newly reported for Europe from Greece. Specimens previously referred to as "*T. picaron*" in Central Asia do not belong to that species and are newly described as *Thyreus jansseni* Wood, **sp. nov.** (Kyrgyzstan and Afghanistan). A further new species in the *scutellaris* group is described, *Thyreus impressus* Wood, **sp. nov.** (Kyrgyzstan). A modified and updated identification key to the 12 European members of the genus is presented, with the aim of stimulating work on this challenging bee genus.

Key Words

DNA barcoding, host-parasite relationship, identification key, museum collections, new species

Introduction

The genus *Thyreus* is the most species-rich member of the obligately parasitic bee tribe Melectini, with about 115 species known across the Old World, representing approximately 55% of the known species richness (Michener 2007; Ascher and Pickering 2025). Melectine bees present numerous taxonomic issues, both in terms of how genera are defined and recognised (e.g. Lieftinck 1972, 1983; Rightmyer and Engel 2003; Michener 2007; Onuferko et al. 2021; Orr et al. 2024) and at the species level. Due to their parasitic nature, predominantly attacking bees of the subfamily Anthophorinae (see Bossert et al. 2019; Orr et al. 2024), melectine species exhibit

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largely conserved and homogeneous morphology, rendering species recognition and delineation challenging.

As the largest genus of Melectini, this statement naturally applies to *Thyreus*. The genus was in a largely chaotic state until the revisionary works of Lieftinck (mainly 1959a, 1962, 1968), who dealt with the Palaearctic, Indo-Malayan, and Australasian faunas. Lieftinck never addressed the Afrotropical fauna, and whilst a revision has been conducted (Eardley 1991), additional work is needed due to the long history of study, ancient type material, and complex nature of the genus. Within the Palaearctic fauna, Lieftinck's (1968) revision resolved many long-running issues. Older works such as Meyer (1921), published before Lieftinck's revision, are largely unusable due to the high degree of taxonomic uncertainty, lack of type revision, taxa described from material that is now lost, and generally muddled concepts; this can be seen when examining historical specimens identified by Meyer, these often being completely misidentified (TJW, pers. obs.). De Beaumont (1940) made a major contribution by working on the West European fauna and clarifying the incorrect application of the name *Thyreus scutellaris* (Fabricius, 1781), and these improvements were cemented by Lieftinck's more comprehensive work.

Since then, the genus has received relatively little taxonomic attention in the Palaearctic (Marikovskaya 1992; Schwarz 1993), with comparatively more attention paid to the Afrotropical fauna (Eardley 1991; Straka and Engel 2012; Alqarni et al. 2014; Engel 2014). However, recent work has demonstrated genuine range expansions (Schmid-Egger et al. 2022) and taxonomic complexity (Wood 2023) in the fauna of Europe and the Mediterranean basin. There has also been an opportunity to study the West and Central Palaearctic fauna using DNA barcodes, which provided both clarity and introduced new complexity. The purpose of the present work is to present these new data on the genus *Thyreus* in the West and Central Palaearctic and to produce an improved identification key to the European fauna in order to stimulate new work on this complex group.

Methodology

Genetics

Collected West and Central Palaearctic *Thyreus* specimens were barcoded using different techniques. For most specimens (sequence prefix WPATW), a single midleg was removed from pinned specimens and sent to the Canadian Centre for DNA Barcoding (CCDB) in Guelph, Canada, for DNA extraction and sequencing; specimens were sequenced following standardised high-throughput protocols (Ivanova et al. 2006). BeeCox1F1/BeeCox1R2 primers (Bleidorn and Henze 2021) were used to target the COI-5 region. Sequences with the prefix BCHYM were generated following the methodology of Schmidt et al. (2015). Sequences with the prefix HYMAA were generated at the University of Neuchâtel, Switzerland, following the methodology outlined in Praz et al. (2019), using the forward primers LepF or UAE3 with the reverse primer LepF (see Praz et al. 2019).

Phylogenetic trees were supplemented with additional published sequences (e.g. Schmidt et al. 2015; Wood 2023; Wood et al. 2024) that were downloaded from GenBank (https://www.ncbi.nlm.nih.gov/genbank/) and the Barcode of Life Data System. Also used were newly generated sequences from the Biodiversity Genomics Europe project, based on specimens from the Naturalis Biodiversity Center that were selected and curated by TJW. Sequences are available at: https://portal.boldsystems.org/result?query=BGENL[recordsetcode]. Taxa were selected from within the West and Central Palaearctic framework of this study (defined below), without including any of the many additional available extralimital sequences of *Thyreus*. Sequences were aligned using MAFFT (Katoh and Standley 2013). Aligned sequences were analysed in Seaview (Gouy et al. 2010) using a maximum-likelihood analysis, which was run with 1,000 bootstraps. Intra- and interspecific distances were calculated using MEGA-X (Kumar et al. 2018).

Morphological and taxonomic concepts

Morphological terminology follows Michener (2007), except for the marginal "zones" of the terga, which are referred to as marginal "areas"; antennomeres, which are numbered 1–12 (female) and 1–13 (male) and abbreviated as "A"; and the use of the word "rhinaria" to refer to the impressed pits on the posterior face of the antennal segments (see Lieftinck 1968). Metasomal terga are abbreviated as "T", and metasomal sterna as "S". For one diagnosis, the relative breadth of the scutellum is presented. This was measured as the distance between the apical points of the axillae (the breadth, i.e. the maximum width of the scutellum) divided by the distance between the base of the scutellum (straight junction with the scutum) and the posterior scutellar points (the length, i.e. the maximum length of the scutellum). Measurements were obtained from photographs, not using a calibrated microscope, and hence are presented as a ratio.

Unless explicitly stated, all specimens were identified by TJW. An identification key is presented for *Thyreus* species occurring in Europe as defined in Ghisbain and Rosa et al. (2023), to facilitate their identification. Put simply, this includes Europe east to the Ural Mountains, European Russia south to but not including the North Caucasus, Turkey in Europe (east to the Bosporus), all Mediterranean islands including Cyprus, and the Macaronesian islands excluding the Cape Verde islands. Whilst the West and Central Palaearctic are poorly and inconsistently defined in the literature, from the perspective of the genus *Thyreus*, these two areas together are considered to include North Africa, the Arabian Peninsula, Iran, and Central Asia (all "-stan" countries, including Afghanistan and Pakistan).

Photographs were taken using an Olympus E-M1 Mark II with a 60 mm macro lens. Additional close-ups were taken with the addition of a Mitutoyo M Plan Apo

10X infinity-corrected objective lens in combination with an Olympus M.Zuiko 2× teleconverter lens, a 10 mm Kenko DG extension tube, and a Meike MK-P-AF3B 10 mm extension tube. Photographs were stacked using Helicon Focus B (HeliconSoft, Ukraine), and plates were prepared in GNU Image Manipulation Program (GIMP) 2.10. Post-processing of some images was carried out in Photoshop Elements (Adobe Systems, USA) to improve lighting and highlight specific characters.

Results are presented in the following order: (1) genetics, (2) description of new species, (3) problematic taxa identified by genetic study, (4) description of missing sexes, (5) new distributional data and range clarifications, and (6) new identification key for European species. In the summary of distributions, new country records are marked with an asterisk "*". New data on host relationships are presented for individual species where sufficient information is available to draw convincing conclusions.

Abbreviations of specimen repositories

CSE	Personal collection of Christian Schmid-Egger, Berlin, Germany
EDC	Personal collection of Eric Dufrêne, Saint-Hippolyte-du-Fort, France
KJCB	Personal collection of Kobe Janssen, Zonhoven, Belgium
LRC	Personal collection of Francisco La Roche, San Cristóbal de La Laguna, Tenerife, Spain
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHN	Muséum national d'Histoire naturelle, Paris, France
MSNG	Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy
NHMD	Natural History Museum of Denmark, Copenhagen, Denmark
NHMUK	Natural History Museum, London, United Kingdom
NMB	Naturhistorisches Museum Bern, Bern, Switzerland
NHMW	Naturhistorisches Museum Wien, Vienna, Austria
OÖLM	Oberösterreichisches Landesmuseum, Linz, Austria
OUMNH	Oxford University Museum of Natural History, Oxford, United Kingdom
RMNH	Naturalis Biodiversity Center, Leiden, the Netherlands
TJWC	Personal collection of Thomas J. Wood, Leiden, the Netherlands
VLC	Personal collection of Vincent Leclercq, Dijon, France
WHLC	Personal collection of Wolf-Harald Liebig, Bad Muskau, Germany
ZMHB	Museum für Naturkunde, Berlin, Germany
ZSI	Zoological Survey of India, Kolkata, India

Results

Genetics

Two main clades were observed in the COI barcode tree (Fig. 1). The first had bootstrap support of 97 and contained the most commonly collected and observed West and Central Palaearctic *Thyreus* species, such as *T. histrionicus* (Illiger, 1806) and *T. ramosus* (Lepeletier, 1841). The second group had bootstrap support of 87 and contained *T. affinis* (Morawitz, 1873), *T. elegans* (Morawitz, 1877) *sensu lato*, a newly described species *Thyreus impressus* Wood, sp. nov., and *Thyreus scutellaris*; this clade is best referred to as the *scutellaris*-group (*sensu* Lieftinck 1968). From the RMNH collection, it was possible to generate a long 1,498 bp sequence from a specimen of *T. scutellaris* from Ufa in southern European Russia (BGENL2290-24), which was included in Lieftinck's (1968: 46) revision. *Thyreus scutellaris* was separated from its nearest neighbour, *T. impressus*, by an average genetic distance of 8.05% (range 8.05–8.05%). The new species *T. impressus* was strongly separated by 10.63% (range 10.33–10.96%) from *T. elegans sensu lato* and by 9.74% from *T. affinis* (range 9.57–9.88%). For *T. elegans*, four barcodes were generated. Specimens from Morocco, the United Arab Emirates, and Iran showed similar barcodes, separated by an average of 1.12% (range 1.07–1.22%). However, the specimen from south-eastern Kazakhstan (Shonzhy) was strongly separated from these three sequences by an average of 10.75% (range 10.49–10.96%). The issues associated with *T. elegans sensu lato* are discussed below.

Within the clade of more commonly collected *Thyreus* species ("Other species of *Thyreus* Panzer" in Lieftinck 1968), results from *T. picaron* Lieftinck, 1968 and *T. truncatus* (Pérez, 1884) require investigation. *Thyreus picaron* sequences from Spain, Italy, Albania, and Iran formed a monophyletic group with average intraspecific variation of 0.31% (range 0.00–0.76%), receiving bootstrap support of 100. This group differed from the single *T.* aff. *picaron* sequence from Kyrgyzstan by an average of 6.58% (range 6.40–6.69%), with the Kyrgyz sequence not falling immediately adjacent to the *T. picaron* cluster. It is described below as *Thyreus jansseni* Wood, sp. nov.

For *T. truncatus*, the picture was complex. Three clades were observed (Fig. 1). The first contained specimens from central Spain, which received bootstrap support of 97; this can be referred to as the "Iberian lineage". The second contained specimens from south-western France (Aude) and south-eastern France (Bouches-du-Rhône), which received bootstrap support of 88; this can be referred to as the "French lineage". Finally, the third contained specimens from southern France (Gard), Switzerland, Germany, Poland, and Kyrgyzstan and received bootstrap support of 96; this can be referred to as the "Euro-Siberian lineage". Variation within lineages was low: an average of 0.21% (range 0.15–0.31%) in the Iberian lineage, 0.00% in the French lineage, and 0.35% (range 0.00–0.83%) in the

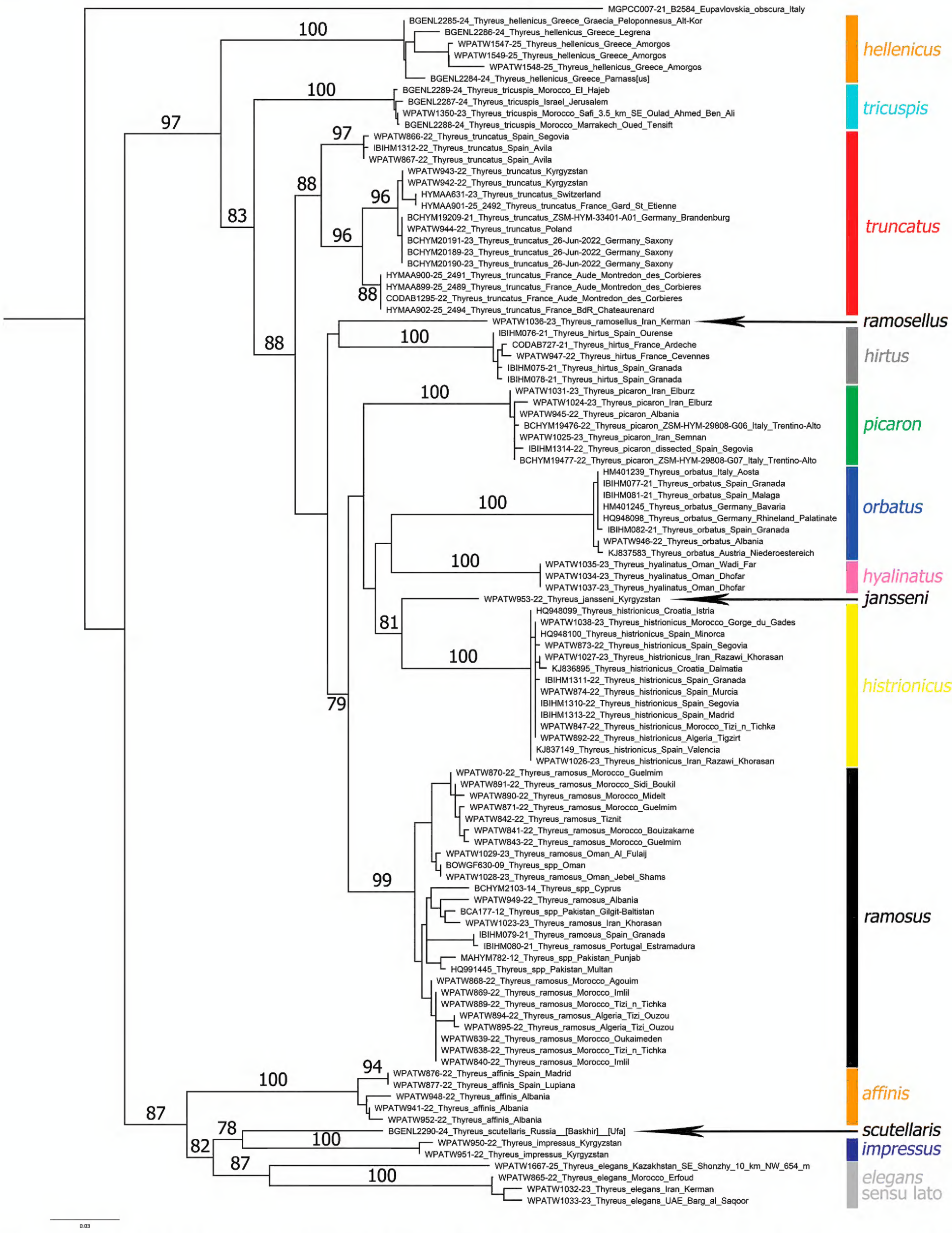

Figure 1. Phylogenetic tree (maximum likelihood) of *Thyreus* Panzer, 1806 species, based on fragments of the mitochondrial COI gene. *Eupavlovskia obscura* (Friese, 1895) is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values < 75% are omitted).

Euro-Siberian lineage, resulting in the high observed bootstrap supports. Variation between clades was 3.80% (range 3.50–4.16%) between the Iberian and Euro-Siberian clades, 3.31% (range 3.12–3.48%) between the Iberian and French clades, and 1.79% (range 1.53–2.13%) between the French and Euro-Siberian clades. All other species in the group of commonly collected *Thyreus* received bootstrap support between 97 and 100 and were well defined genetically.

New species descriptions

Thyreus jansseni Wood, sp. nov.

https://zoobank.org/37102F10-26D5-4F30-AAF3-64FAC7D3EC1A

Type materials. ***Holotype*: Kyrgyzstan** • 1♂; Kirpichny; 42.4047°N, 77.8645°E; 11 Jul. 2019; K. Janssen leg.; RMNH; RMNH.INS.1714348 (BOLD accession number WPATW953-22).

***Paratypes*: Afghanistan** • 2♂; Ghazni province, Jaghori district; 30 Jun. 1997; G.G.M. Schulten leg.; RMNH; ZMA.INS.5144956–ZMA.INS.5144957; **Kyrgyzstan** • 1♂; Narynskaya, Distr. Dzhumgalsky, S Kyzyl-Oy; 1750–1800 m a.s.l.; 5–6 Jul. 1996; H. Rausch leg.; OÖLM.

Diagnosis. *Thyreus jansseni* can be recognised as a typical *Thyreus* ("Other species of *Thyreus* Panzer") due to the large flattened scutellum which posteriorly projects over the metanotum and which is uniformly flattened over its entire surface and which is not medially sulcate (Fig. 2C), combined with the genital capsule with a large gonostylus which is covered with long hairs (Fig. 3G). Due to the white hairs on T1 which form C-shaped patches (Fig. 3C; basally slightly incurving towards the scutellum), the scutellum with punctures separated by 0.5–1 puncture diameters and with polished shining interspaces (Fig. 2C), with S8 produced into two projections which are apically truncate and which curve laterally, thus appearing to be "golf-club"-shaped (Fig. 3E), and the genital capsule with a large apically truncate projection and basal dorsally projecting and acutely pointed section oriented roughly 90° relative to the larger lobe (Fig. 3G), it can be confused only with *Thyreus picaron* (Figs 2D, 3D, 3F, 3H).

Thyreus jansseni can be separated from *T. picaron* due to the smaller body size of 10 mm (12–13 mm in *T. picaron*), scutellum 1.5 times wider than long with the median notch barely indicated (Fig. 2C; in *T. picaron* with the scutellum 1.6 times wider than long, and with the median notch deep and strongly indicated, Fig. 2D), antennal segments viewed dorsally with a strong division between the anterior face which is covered with fine shining scales and the dull posterior face (Fig. 2E; in *T. picaron* with a weaker division between the shinier anterior and duller posterior faces of the antenna, Fig. 2F), posterior faces of the antennal segments with very weakly impressed paired rhinaria, those situated more ventrally very difficult to see (in *T. picaron* with the posterior faces of the antennal segments with strongly impressed paired rhinaria, dorsal and ventral rhinaria equally visible), and posterior basitarsus with only a small white hair fringe dorsally (Fig. 3A; in *T. picaron* with the hind basitarsus entirely covered in fine white hairs, these becoming thicker dorsally, Fig. 3B).

Description. Female. Unknown, though likely described by Marikovskaya (1992) as *T. picaron* auctorum (see below).

Male. Body length: 10 mm (Fig. 2A). ***Head*:** Dark, 1.3 times wider than long (Fig. 2B). Clypeus flattened, densely punctate, punctures separated by ≤ 0.5 puncture diameters, surface between punctures shining. Labrum rounded rectangular, almost 2 times longer than wide, apex with elevated subapical transverse carina forming obtusely pointed tooth; labrum basally weakly produced into two tubercles laterally. Gena narrower than width of compound eye; ocelloccipital distance 2 times diameter of lateral ocellus. Hind margin of vertex with narrow obscure slightly raised carina-like rim. Face between antennal insertions with raised longitudinal carina, reducing in height and becoming medial impression on frons anterior to median ocellus. Frons punctate, punctures separated by ≤ 0.5 puncture diameters, becoming sparser in area anterior to median ocellus; vertex behind ocellar triangle densely punctate, areas adjacent to lateral ocelli impunctate, smooth and shining. Face with abundant white pubescence, decumbent on lower half of face below antennal insertions. Gena ventrally with dark hairs, dorsally with scattered white hairs. Antenna dark, A4–13 with anterior faces lightened by presence of greyish scales; posterior faces of A4–13 with fine granular microreticulation, surface dull and strongly contrasting scales of anterior faces (Fig. 2E). Posterior faces of A4–13 with small and superficially impressed paired rhinaria placed close to junction with preceding segment, ventral rhinaria almost undetectable. A3 0.8 times length of A4.

***Mesosoma*:** Scutum and scutellum punctate, punctures separated by 0.5–2 puncture diameters but typically by 1 puncture diameter, surface between punctures smooth and shining. Scutellum 1.5 times wider than long, posterior margin wavy, with small median notch, posteriorly with moderate tuft of white hair projecting from ventral surface (Fig. 2C). Axilla flush with outer margin of scutellum, scutellum and axilla with dark hairs which do not obscure surface. Mesepisternum densely punctate medially, punctures confluent with slightly raised ridges, becoming sparser ventrally, here separated by 0.5–2 puncture diameters. Legs dark, with abundant white pubescence on outer face of tibiae, covering entirety of fore and mid-tibiae and basal ½ of hind tibiae. Hind basitarsus predominantly with dark hairs, dorsal surface with small white hair fringe (Fig. 3A). Forewing weakly infuscate.

***Metasoma*:** Terga dark, tergal discs punctate with hair-bearing punctures, punctures presenting short, posteriorly projecting black plumose hairs; punctures separated by 0.5–1 puncture diameters (Fig. 3C). T1 with L-shaped white hair patch laterally, apically extending further towards centre of tergum than basally, hairs predominantly adpressed, some loose hairs found basolaterally. T2 with almost rectangular patches of white hairs laterally, with narrow extension towards base of disc laterally. T3–5 with rectangular patches of white adpressed hairs, not forming complete bands. T7 with apical margin essentially straight, weakly wavy. S8 delicate, posterior projections with narrow stem before turning 90° degrees to form small laterally projecting discs (Fig. 3E). Genital capsule compact, almost rounded, gonocoxa slightly broadened and truncate apically, in basal part with dorsally projecting acutely pointed lobe rotated 90° relative to truncate section (Fig. 3G). Basal and apical parts of gonostylus covered with long brown hairs, hairs simple apically, weakly plumose basally.

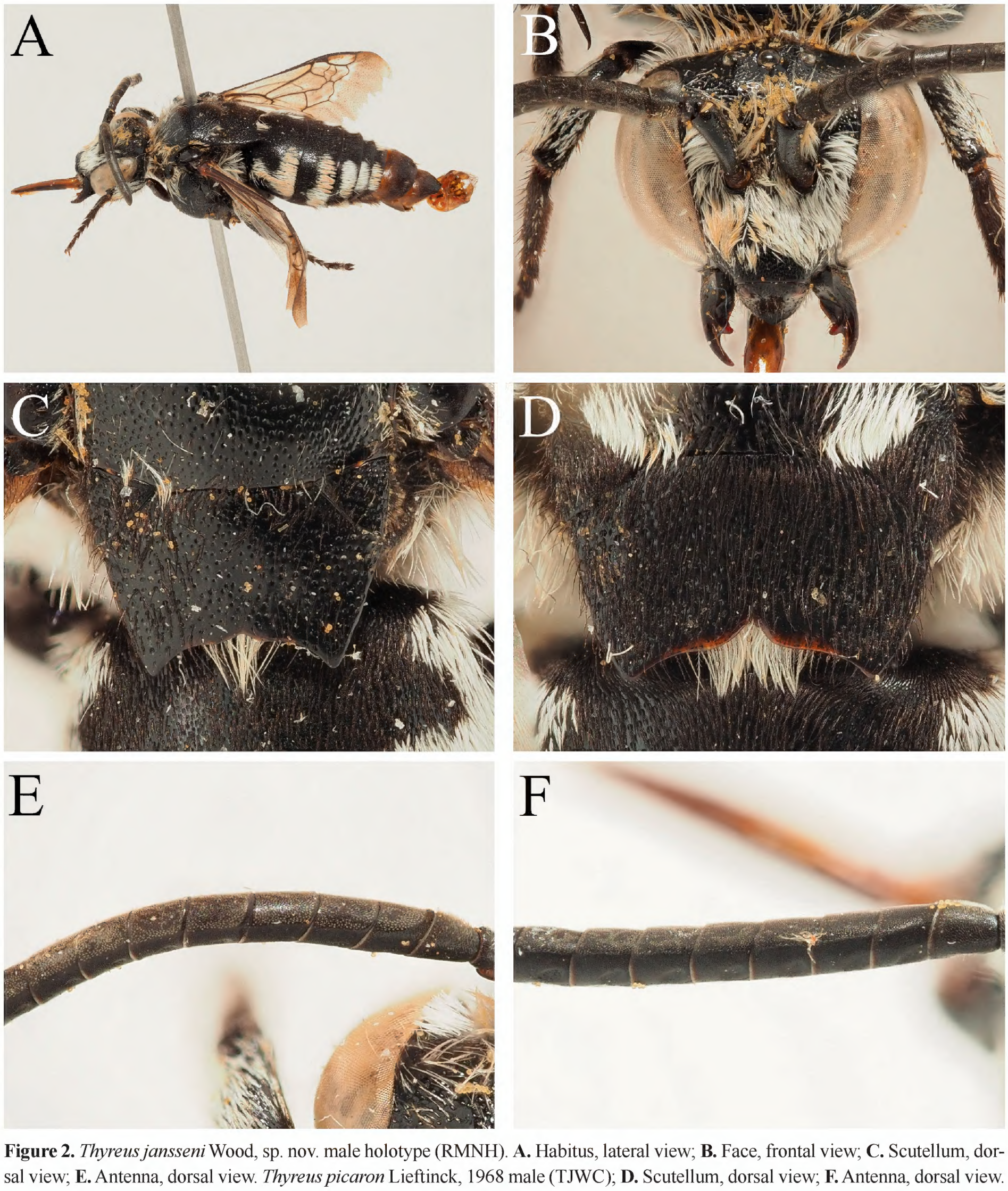

Figure 2. *Thyreus jansseni* Wood, sp. nov. male holotype (RMNH). **A.** Habitus, lateral view; **B.** Face, frontal view; **C.** Scutellum, dorsal view; **E.** Antenna, dorsal view. *Thyreus picaron* Lieftinck, 1968 male (TJWC); **D.** Scutellum, dorsal view; **F.** Antenna, dorsal view.

Notes. Marikovskaya (1992) described the female of "*Thyreus picaron*" from the Alai Mountains in Kyrgyzstan, near the village of Дарaут-Курган (= Daroot-Korgon), with 12♀ and 7♂ specimens collected between 15 and 16 July 1986. Based on Marikovskaya's writing and illustrations, it is highly likely that she was dealing with *T. jansseni* and hence described the female of this species. Unfortunately, Marikovskaya's collection appears to have been destroyed (Pierre Rasmont, pers. comm.), which does not allow us to draw conclusions with certainty. Moreover, Marikovskaya did not give the size of the female or male specimens, but she did indicate that the host of her species was *Anthophora* (*Mystacanthophora*) *borealis* Morawitz, 1865. This species, and indeed the subgenus of bees, is very rare in Europe and is found in temperate to boreal habitats, which do not overlap at all with the observed distribution of *T. picaron* in Europe and the Near East, which is Mediterranean in character. *Anthophora borealis* is typically 10–11 mm in length, which is simply too small to host *T. picaron*, which has males 12–13 mm in length, and females will of course

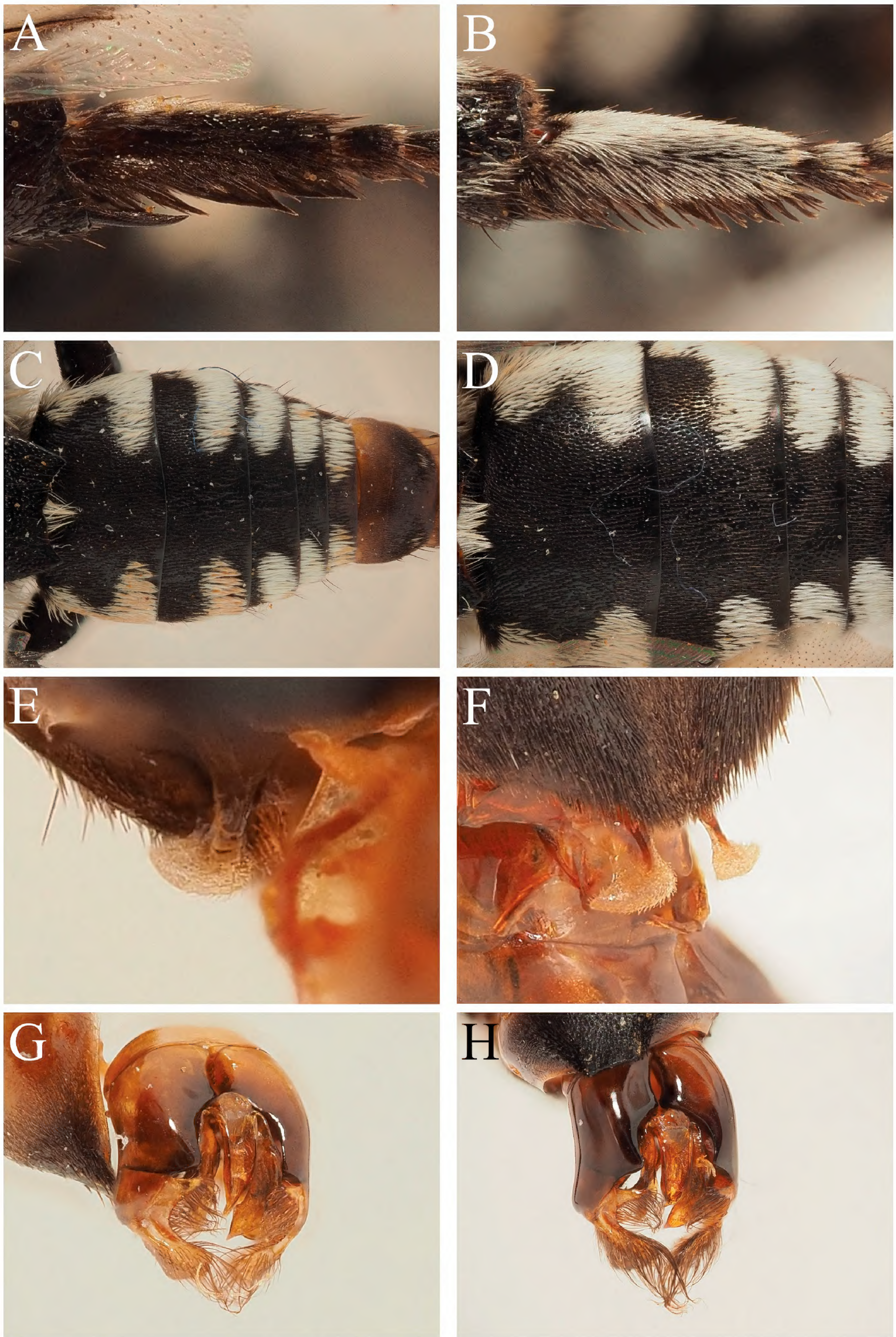

Figure 3. *Thyreus jansseni* Wood, sp. nov. male holotype (RMNH). **A.** Hind basitarsus, lateral view; **C.** Metasoma, dorsal view; **E.** S8, dorsal view; **G.** Genital capsule, dorsal view; *Thyreus picaron* Lieftinck, 1968 male (TJWC); **B.** Hind basitarsus, lateral view; **D.** Metasoma, dorsal view; **F.** S8, ventrolateral view; **H.** Genital capsule, dorsal view.

be slightly larger on average. *Thyreus picaron* is likely attacking larger *Amegilla* (*Amegilla*) species (see below), which would account for its much larger body size relative to *T. jansseni*. *Anthophora borealis* and, possibly other species of *Mystacanthophora* Brooks, 1988, therefore seem to be the likely host(s) of *T. jansseni*.

Etymology. The name is to recognise Kobe Janssen (Belgium), who very generously shared large numbers of bee specimens (including Melectini) with the lead author for a long period of time.

Distribution. Kyrgyzstan and Afghanistan. Likely present in other Central Asian countries, given Lieftinck's (1968: 92) paratypes of *T. picaron* from Uzbekistan (Dzhuma) and Kazakhstan (Zharkent, Kazaly) (specimens in St. Petersburg, Oxford, and Prague). Examination of these specimens is necessary to clearly delineate the distributions of these two species. Searches in the OUMNH (TJW, August 2025) could not locate any "*T. picaron*" specimens or registration of such in the type catalogue.

Thyreus impressus Wood, sp. nov.

https://zoobank.org8E37B113-D55C-4FB7-8874-2A9D628367DE

Type materials. ***Holotype*: Kyrgyzstan** • 1♂; 45 km W of Naryn; 41.4160°N, 75.3969°E; 20 Jul. 2019; K. Janssen leg.; RMNH; RMNH.INS.1714347 (BOLD accession number WPATW950-22).

***Paratype*: Kyrgyzstan** • 1♂; 45 km W of Naryn; 20 Jul. 2019; 41.4160°N, 75.3969°E; K. Janssen leg.; TJWC (BOLD accession number WPATW951-22).

Diagnosis. *Thyreus impressus* can be placed into the *scutellaris*-group due to the genital capsule, which is simple, with the gonostylus greatly reduced in size and pointed-triangular without an additional dorsal projection (Fig. 5E), and the gonostylus with only a few inconspicuous hairs. It can be separated from all other members of the group except *T. scutellaris* by the structure of the scutellum, which is medially impressed and sulcate, with the axillae slightly diverging from the outer margins of the scutellum and produced into slight but distinct points (Fig. 4C), and due to the white hair patches at the base and on the marginal area of T1, both widely separated medially and laterally by abundant black hairs, thus forming 4 distinct patches in dorsal view (Fig. 4D).

The two species are similar, but *T. impressus* can be recognised due to the gonostylus which is small and acutely pointed, with the inner margin straight (Fig. 5E; in *T. scutellaris* with the gonostylus more elongate and apically blunt to rounded, and the inner margin with a distinct subapical kink, Fig. 5F; see also illustration in Lieftinck 1968: 46), in frontal view with A3 only slightly exceeding A4 in length (Fig. 5A; in *T. scutellaris* with A3 clearly exceeding A4 in length, approaching A4+5, Fig. 5B), and the posterior faces of the antennal segments with strongly produced

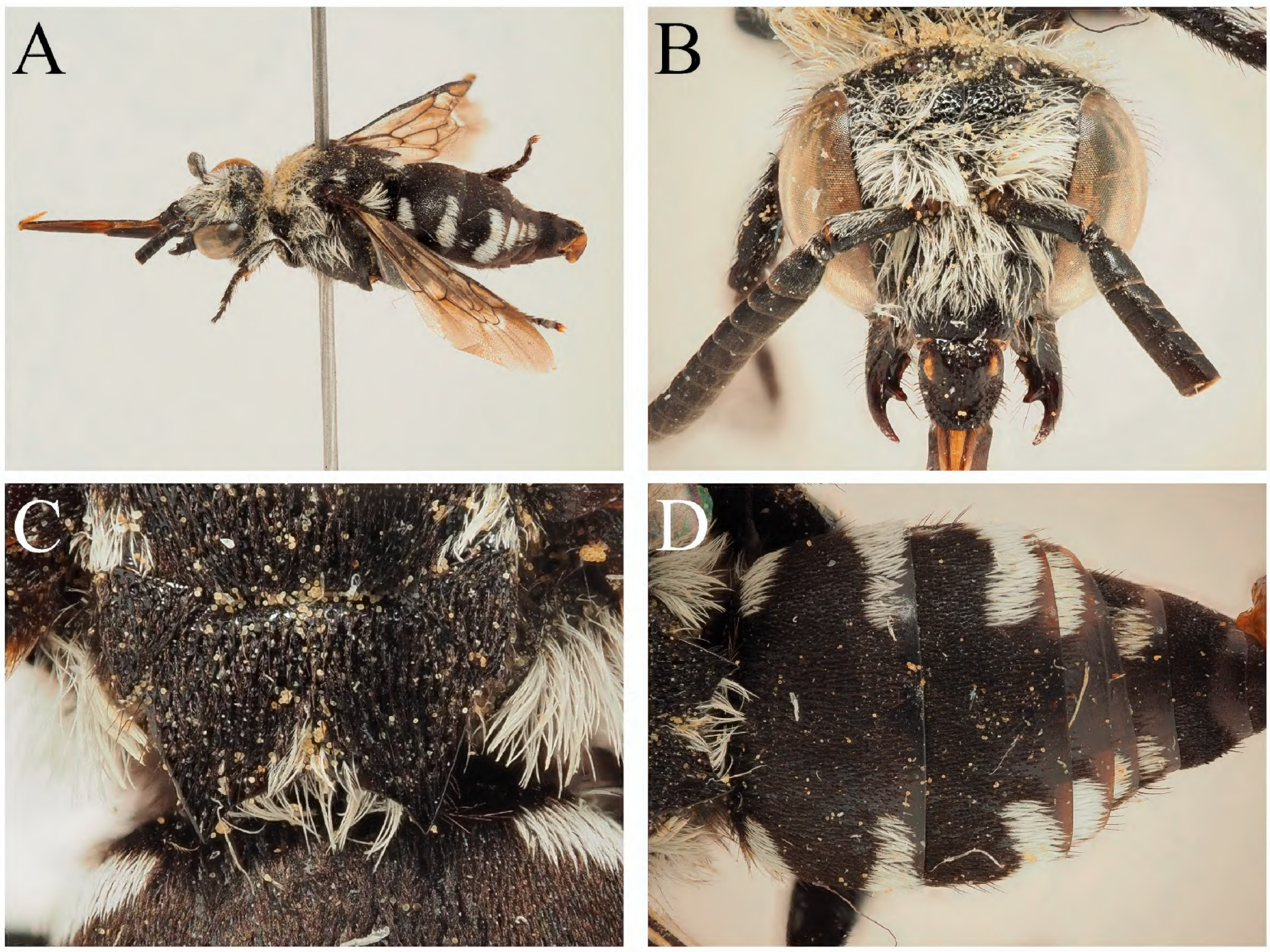

Figure 4. *Thyreus impressus* Wood, sp. nov. male holotype (RMNH). **A.** Habitus, lateral view; **B.** Face, frontal view; **C.** Scutellum, dorsal view; **D.** Metasoma, dorsal view.

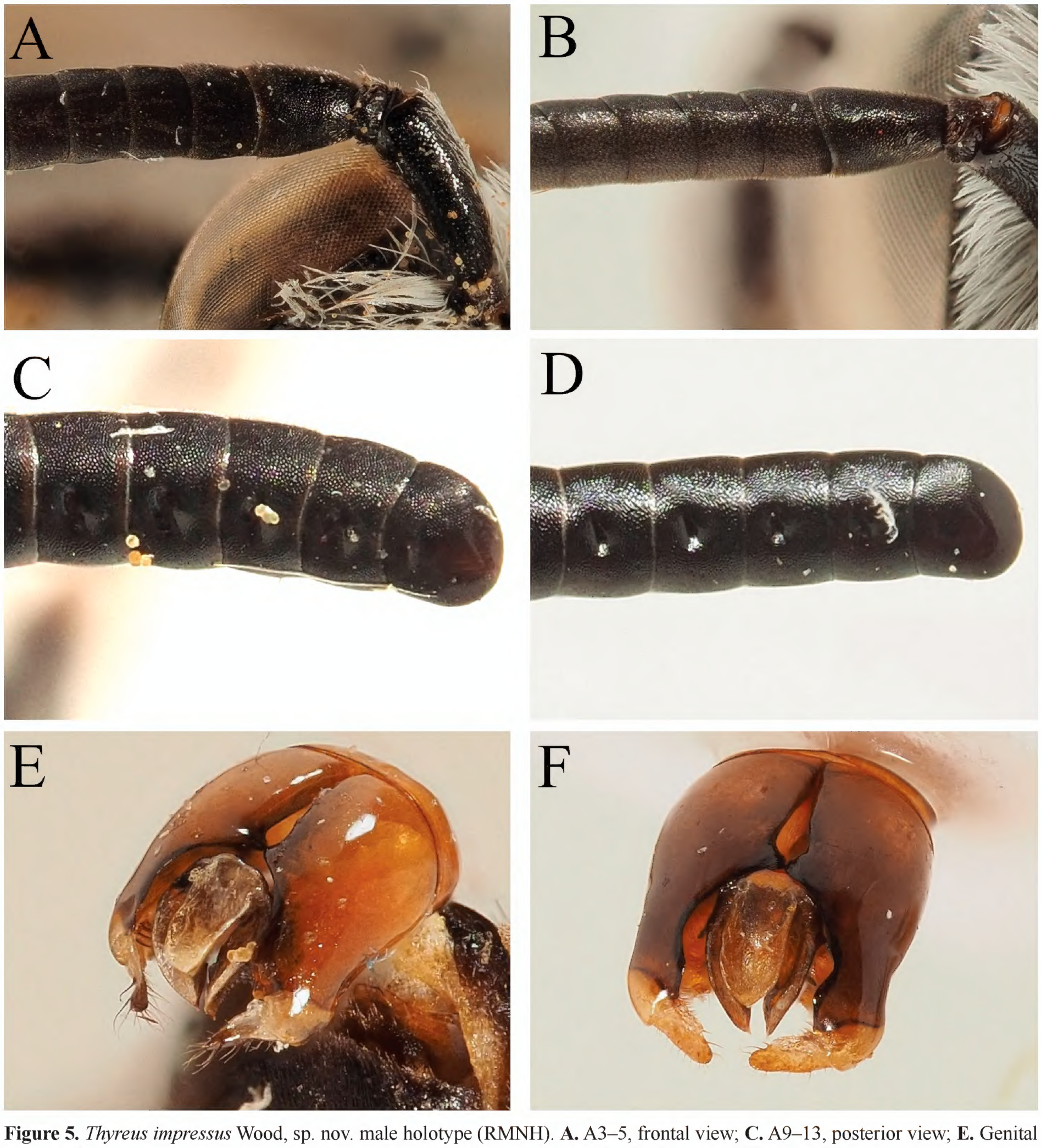

Figure 5. *Thyreus impressus* Wood, sp. nov. male holotype (RMNH). **A.** A3–5, frontal view; **C.** A9–13, posterior view; **E.** Genital capsule, detail of gonostylus, dorsolateral view; *Thyreus scutellaris* (Fabricius, 1781) male (TJWC); **B.** A3–5, frontal view; **D.** A9–13, posterior view; **F.** Genital capsule, detail of gonostylus, dorsal view.

individual rhinaria (not paired), clearly visible on the posterior face of A13 (Fig. 5C; in *T. scutellaris* with the posterior faces of the antennal segments with weakly produced individual rhinaria, that on A13 so small and weak as to not be immediately visible, Fig. 5D).

Description. Female. Unknown.

Male. Body length: 9.5–10 mm (Fig. 4A). ***Head*:** Dark, 1.25 times wider than long (Fig. 4B). Clypeus flattened, densely punctate, punctures confluent, surface dull with exception of narrow shining margin. Labrum rounded rectangular, 1.5 times longer than wide, apex with elevated subapical transverse carina forming obtusely pointed tooth; labrum basally weakly produced into two tubercles laterally. Gena narrower than width of compound eye; ocelloccipital distance 1.5 times diameter of lateral ocellus. Hind margin of vertex with narrow obscure slightly raised carina-like rim. Face between antennal insertions with weak raised longitudinal carina, rapidly reducing in height and becoming medial impression on frons anterior to median ocellus. Frons punctate, punctures separated by ≤ 0.5 puncture diameters, punctation becoming slightly weaker on vertex, here separated by up to 1 puncture diameter. Face with abundant white pubescence, decumbent on lower half of face below antennal insertions.

Gena ventrally with dark hairs, dorsally and laterally with scattered white hairs. Antenna dark, with very fine granular microreticulation, A3 slightly exceeding A4, shorter than A4+5 (Fig. 5A). Posterior faces of A3–13 with strongly impressed individual rhinaria (Fig. 5C).

***Mesosoma*:** Scutum and scutellum densely punctate, punctures separated by ≤ 0.5 puncture diameters, interspaces slightly shining. Scutellum 1.6 times wider than long, posterior margin widely emarginate, medially distinctly impressed and sulcate (Fig. 4C) with dorsal and ventral tufts of white hairs; axillae with outer margins slightly but distinctly diverging from outer margins of scutellum and produced into slight but distinct points. Remaining surface of scutellum and axilla covered with dark hairs which do not obscure surface. Mesepisternum densely punctate, punctures separated by 0.5–1 puncture diameter. Legs dark, with white pubescence on outer face of tibiae, covering entire length on all tibiae. Forewing weakly infuscate.

***Metasoma*:** Terga dark, tergal discs densely punctate with hair-bearing punctures, punctures presenting short, posteriorly projecting black plumose hairs; punctures separated by ≤ 0.5 puncture diameters. T1 with 4 patches of white hairs laterally, 2 basally and 2 apically, patches widely separated by black hairs on lateral margins of terga (Fig. 4D). T2 with almost rectangular patches of white hairs laterally, with clear but narrow extension towards base of disc laterally. T3–5 with rectangular patches of white adpressed hairs, not forming complete bands. T7 with apical margin shallowly and evenly emarginate. Genital capsule compact, rounded, gonostylus greatly reduced in size and pointed-triangular without additional dorsal projection (Fig. 5E). Gonostylus with only scattered inconspicuous hairs.

Etymology. Masculine nominative singular form of the Latin adjective *impressus* meaning impressed, in reference to the more strongly produced antennal rhinaria compared to *T. scutellaris*.

Distribution. Kyrgyzstan.

Taxa presenting taxonomic complexity based on barcode analysis

Thyreus elegans (Morawitz, 1877)

Crocisa elegans Morawitz, 1877: 101, ♀ [Azerbaijan, type lost].

?Crocisa intrudens Smith, 1878: 6, ♀ [China: Yarkant, ?ZSI, not examined].

?Crocisa laevicrus Morawitz, 1886: 222, ♂ [China: Niya, type lost].

Crocisa quadridentata Saunders, 1908: 266, ♂ [Algeria, NHMUK, examined].

Crocisa brezzii Guiglia, 1933: 140, ♀ [Libya, MSNG, examined].

Material examined (illustrative). **Algeria** • 1♂; Biskra; 13 May 1897; A.E. Eaton leg.; NHMUK (***holotype*** of *C. quadridentata*); **Kazakhstan** • 7♂; SE, Shonzhy 10 km NW; 654 m a.s.l.; 2 Jun. 2024; C. Schmid-Egger & W-H. Liebig leg.; CSE/TJWC/WHLC (BOLD accession number WPATW1667-25); **Iran** • 1♂; Kerman prov., 7.5 km NE Shahdad; 8 May 2019; C. Schmid-Egger leg.; TJWC (BOLD accession number WPATW1032-23); **Libya** • 1♀; Gialo [Jalu]; 1–30 Jun. 1931; Miss. Zool. aCufra leg.; MSNG (***holotype*** of *C. brezzii*); **Morocco** • 1♀; Erfoud, Jorf; 5 Jul. 2019; P. Rasmont leg.; TJWC (BOLD accession number WPATW865-22); **United Arab Emirates** • 1♀; Barg al-Saqoor; 30 Apr. 2019; A. van Harten leg.; TJWC (BOLD accession number WPATW1033-23).

Notes. *Thyreus elegans* was described from Kurgulutschaiskaja and Tschemachlinskaja (Morawitz 1877) in modern-day Azerbaijan; without topotypic sampling, it is not currently possible to confidently assign the name to either of the two clades observed in *T. elegans sensu lato*. It is not impossible that additional sampling between central Iran and south-eastern Kazakhstan may demonstrate that this genetic difference is simply intraspecific variation, although this is considered unlikely, as a 10% difference in COI is substantial based on the pattern observed here in *Thyreus* species (Fig. 1). However, Lieftinck (1968: 131) commented on the name *Thyreus laevicrus* (Morawitz, 1886), which was described from "Oasis Nia, Tibet", most likely corresponding to Niya in Xinjiang, China. The holotype male is lost, and Lieftinck expressed doubts as to whether *T. laevicrus* was distinct or simply a variety of *T. elegans*. The modern sample of "*T. elegans*" from Shonzhy is approximately 700 km from Niya. It may therefore represent a valid species, but it is premature to recognise it currently, especially since no morphological characters are apparent in the male sex, the only sex currently available from this sampling locality. Lieftinck (1968: 131) mentioned that the more slender pygidial plate of females could be used to distinguish Siberian and Central Asian specimens from Cypriot specimens, but this requires further study.

Moreover, the type of *Thyreus intrudens* (Smith, 1878), described from Yarkand [Yarkant County] in western China, should be searched for in the Zoological Survey of India collection (Kolkata), as the name would have priority over *T. laevicrus* if its identity can be clarified. Other type specimens from Smith (1878) have been located in the ZSI (e.g. Gautam et al. 2024), and it seems the most likely type repository (see Baker 1993: 272). The illustration provided by Smith (1878: fig. 8) shows a melectine bee with four white patches of pubescence on T1, thus resembling *T. elegans* in a general sense. The description is highly suggestive, referring to "the scutellum deeply emarginate and having a little white pubescence in the emargination" and "Abdomen, a broad band of white pubescence at the base and a narrower one on the apical margin of the segments, all slightly interrupted in the middle". See also comments by Baker (1993: 276).

Distribution. West and Central Palaearctic; precise details are given by Lieftinck (1968) & Wood and Bossert (2025).

Thyreus truncatus (Pérez, 1884)

Crocisa truncata Pérez, 1884: 312, ♂ [France, MNHN, examined] (Fig. 6).
Crocisa ramosa var. *mucorea* Friese, 1925: 30, ♀ [Egypt, ZMHB, examined] (Fig. 7).
Crocisa nadigi Alfken, 1933: 136, ♀♂ [Morocco, ZMHB, examined] (Fig. 8).
Crocisa curviscutum Alfken, 1934: 167, ♀♂ [Egypt, ZMHB, examined] (Fig. 9).

Material examined. **Egypt** • 1♀; Heliop. [Heliopolis]; 21 Apr. 1896; O. Schmiedeknecht leg.; ZMHB (***holotype*** of *Crocisa ramosa* var. *mucorea*) • 3♀; Pyramids; 12 May 1914; Adair leg.; ZMHB (***holotype*** and ***paratypes*** of *Crocisa curviscutum*); **France** • 1♂; Mpeli [Montpellier], 980 [Pérez catalogue number]; MNHN (***lectotype*** by present designation); **Kyrgyzstan** • 2♂; 50 km W Naryn; 21 Jul. 2019; K. Janssen leg.; KJCB • 1♂, 1♀; 45 km W Naryn; 20 Jul. 2019; K. Janssen leg.; TJWC; **Moldova** • 2♂; Kišiněv [Chişinău]; 1–30 Jun. 1995; I. Pavilčok leg.; OÖLM; **Morocco** • 1♂, 2♀; El Hajeb; 22 Jul. 1932; Ad. Nadig leg.; ZMHB (male ***holotype***, female ***paratypes*** of *Crocisa nadigi*). Additional examined specimens are detailed in Suppl. material 1.

Notes. Lieftinck (1968) gave the publication year of *Crocisa truncata* as 1883, but Baker (1996) identified that the work of Pérez (*Contribution à la faune des apiaires de France. Deuxième Partie*) was published in three tranches, with pages 257–320 issued in February 1884. The description of *T. truncatus* was therefore published in 1884. A single syntype was preserved in the MNHN until at least the 1930s, as it was inspected by de Beaumont (1940: 167), but seemingly not by Lieftinck (1968). Moreover, de Beaumont (1940) did not indicate the label information of this syntype, which is important because Pérez (1884) described the species from "Provence et Languedoc". In the unpublished catalogue of Pérez (https://science.mnhn.fr/catalogue/ey-bib-perez1/), on page 164, species entry 980 lists: "*Crocisa truncata* J.P. Montpellier *1♂*". This syntype was located during a recent visit to the MNHN in September 2025 (Fig. 6); it is indeed a male specimen from Montpellier bearing the catalogue number 980 (Fig. 6A) and is hereby designated as the lectotype. It is not dissected, but the short scutellum is clearly visible (Fig. 6C), confirming the current interpretation of the species in a general sense.

DNA barcoding analyses revealed three mitochondrial lineages within *Thyreus truncatus sensu lato*: an Iberian lineage, a Euro-Siberian lineage, and a French lineage (Fig. 1). These lineages were separated by genetic distances of between 1.53 and 4.16%. Two of these lineages are present in the south of France, the *terra typica* of *T. truncatus*: the widespread Euro-Siberian lineage (east to Kyrgyzstan), which descends from Switzerland along the Rhône River to Saint-Étienne-des-Sorts (Département Gard), and just 35 kilometres further south, at Châteaurenard (Département Bouches-du-Rhône), the French lineage is detected. This second lineage is also found in Montredon-des-Corbières (Département Aude) in south-western France. Based on collecting locality, the lectotype of *T. truncatus* would probably belong to the French mitochondrial lineage, but topotypic sampling is required.

Morphologically, based on barcoded specimens examined for morphology, specimens from the Iberian and Euro-Siberian lineages appear separable in some cases (Table 1), particularly with reference to the male genitalia and the density of punctation on the outer face of the apex of the gonostylus. However, specimens from France, including those from the French lineage and the lone barcoded specimen from the Euro-Siberian lineage (specimen number 2492 in Fig. 1), display an intermediate morphology in puncture density.

Given the inability to recognise three consistently and morphologically distinct forms, with specimens from southern France presenting an intermediate morphology; the presence of at least two mitochondrial lineages in close proximity in southern France; and the lack of genetic data from Egypt and Morocco – the countries from which the names with the next oldest priority arise (Figs 7–9) – any taxonomic action at the present time presents a serious risk of nomenclatural instability. It may be the case that Iberian "*T. truncatus*" could be treated as *T. nadigi* in a future revision, but this is currently premature. We therefore take no action and maintain a broad concept of *T. truncatus*, in line with the concept and synonymies established by Lieftinck (1968), pending further study. Such future studies should further investigate species delimitation in this widespread taxon, delineate the distribution of the two mitochondrial clades found in France, and examine morphological variation with longer series of specimens.

Table 1. Morphological characters that can provisionally be used to separate the Iberian and Euro-Siberian mitochondrial lineages of *T. truncatus* (Pérez, 1884).

Body part	Iberian *T. truncatus*	Euro-Siberian *T. truncatus*
Male gonostylus, outer face of apical part	Densely punctate before slight impression, shorter, appearing rounded	Weakly punctate, gonostylus longer, thus appearing more parallel sided
Male and female hind tibiae	Apex with surface shiny between short spines	Apex dull between short spines
Female tergal rims	Marginal areas with rims shiny; most obvious on T5	Marginal areas with rims dull
Female tergal rims	Marginal areas with rims broadening medially	Marginal areas with rims of uniform width across their breadth
Female labrum	Labrum with medial tooth dull	Labrum with medial tooth polished and shining, sharply produced

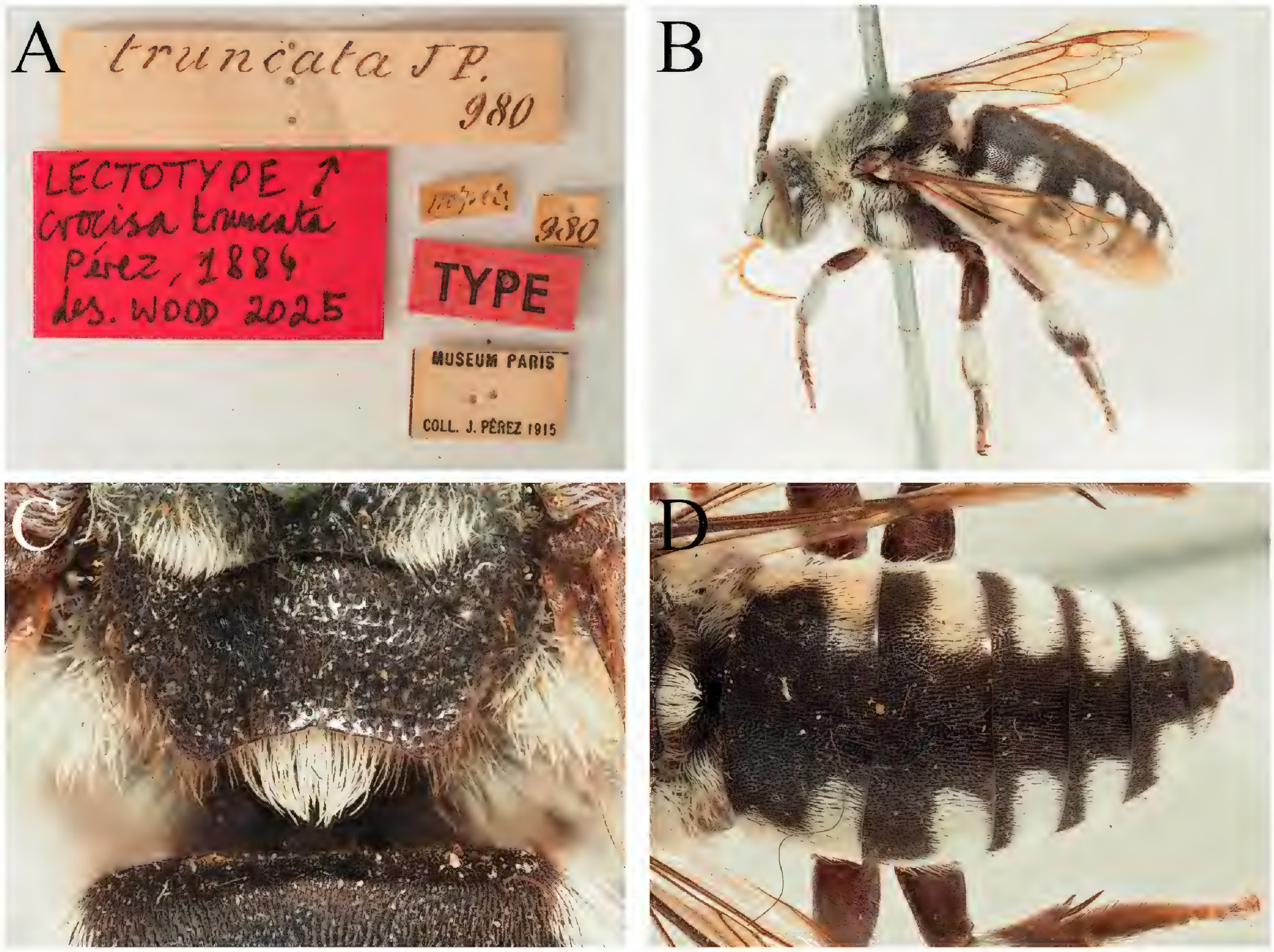

Figure 6. *Thyreus truncatus* Pérez, 1884 male lectotype (MNHN). **A.** Label details; **B.** Habitus, lateral view; **C.** Scutum, dorsal view; **D.** Metasoma, dorsal view.

Ecologically, the host in at least the German and Austrian parts of its range is *Tetralonia dentata* (Germar, 1839) (Schmid-Egger et al. 2022), which has an overall distributional range stretching from Morocco to Central Asia (GBIF.org 2025). Collections in Spain (TJW) have produced *T. truncatus* at sites where *Te. dentata* was caught abundantly (provinces of Segovia in 2019 and Ávila in 2020), and *Te. dentata* is often present with *T. truncatus* in southern France (M. Aubert, pers. comm.). One female of *T. truncatus* was collected flying over a nesting site of *Te. dentata* in southern France (CP, M. Aubert and E. Dufrêne, pers. obs.). Overlaying *Te. dentata* distributional data from GBIF, there is a broad correspondence in the distribution (Fig. 10), although GBIF data for *Te. dentata* are lacking for Greece, the Levant, and the Caucasus, areas where this species is known to occur (Kuhlmann et al. 2014; Ascher and Pickering 2025). There are clear areas of close correspondence in central Spain, southern France, south-western Switzerland, eastern Austria, and eastern Germany. However, *Te. dentata* does not appear to have been recorded from Egypt, the *locus typicus* for both *T. mucoreus* and *T. curviscutum*. In general, the distributional similarities are closer in the west but weaker in the east, where greater revision of *Te. dentata* specimen data is required.

Interestingly, *Te. dentata* also shows considerable variation in the COI gene. The sequence of *Te. dentata* published by Wood et al. (2024) from Ávila forms a unique BIN (BOLD: AEO2705) that is separated by approximately 5.4% from a BIN containing *Te. dentata* sequences from France and Switzerland (BOLD: AEE2533), and an additional BIN is formed for German and Hungarian sequences of *Te. dentata* (BOLD: ABA8838). A final BIN was assigned to specimens from Kyrgyzstan that may belong to *Te. dentata* (BOLD: AAI0670). Work is ongoing to understand genetic variation in this nominally widespread host species (VL and P. Biella, unpublished data).

Distribution. Morocco, Algeria, Egypt, Spain, France, Germany, Switzerland, Italy, Austria, Hungary, Czechia, Slovakia, Poland, Slovenia, Croatia, Serbia, Albania, North Macedonia, Romania, Bulgaria, Greece, Moldova*, Ukraine, Belarus, Russia (European part), Turkey, Georgia, Azerbaijan, Israel, Syria, Kuwait, Iran, Tajikistan, Kyrgyzstan* (de Beaumont 1940; Lieftinck 1968; Kuhlmann et al. 2014; Ascher and Pickering 2025; Fig. 10).

Description of missing sexes

Thyreus parthenope Lieftinck, 1968

Thyreus parthenope Lieftinck, 1968: 110, ♂ [Yemen, NHMUK, examined].

Material examined. **Egypt** • 1♀; Egypt [no further information]; 1858; Natt. leg.; NHMW; **Oman** • 1♀; Muscat,

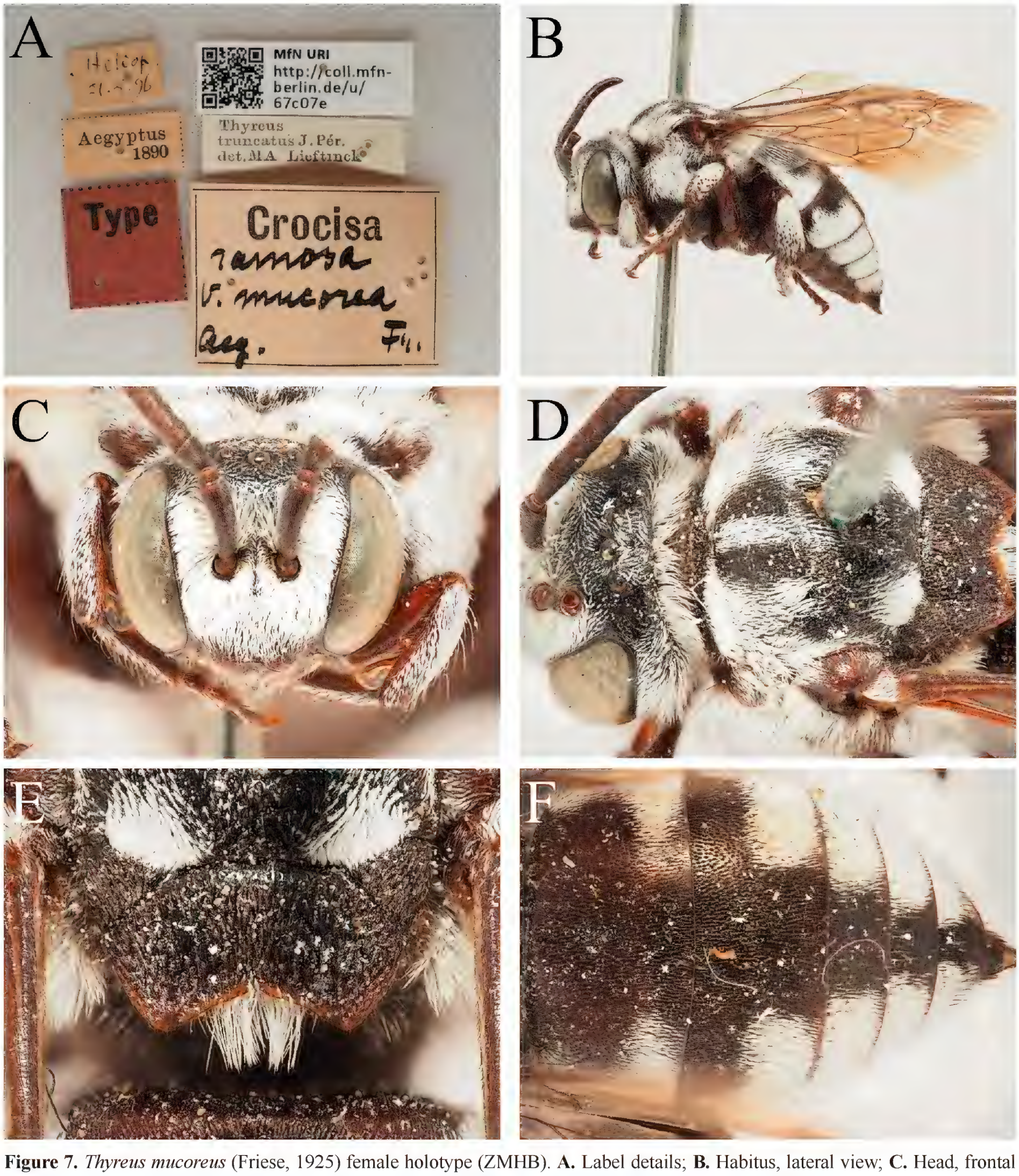

Figure 7. *Thyreus mucoreus* (Friese, 1925) female holotype (ZMHB). **A.** Label details; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Scutum, dorsal view; **E.** Scutellum, dorsal view; **F.** Metasoma, dorsal view.

Ruwi; 1–31 Mar. 1976; K.M. Guichard leg.; NHMUK; **Saudi Arabia** • 4♂; Abu Arish; 25 Mar. 1980; K.M. Guichard leg.; D.B. Baker det. 1981; NHMUK • 2♂; Asir prov., Abha Gov., Jabal Sawda Mts., 5km SE Al Henayah vill.; 22 Oct. 2024; Y. Skrylnyk leg.; VLC • 1♂; Jizan prov., Al-Aydabi Gov., 8.5km S. Al Henayah vill.; 23 Oct. 2024; Y. Skrylnyk leg.; VLC • 7♂; Jizan prov., Fayfa Gov., Jabal Fayfa Mts., 5km SE Al Henayah vill.; 18–19 Mar. 2025; Y. Skrylnyk leg.; TJWC/VLC; **Sudan** • 1♀; Khartoum; 4 Dec. 1991; G.G.M. Schulten leg.; RMNH; **United Arab Emirates** • 1♂; Hatta (hotel); 1 Nov. 1985; I.L. Hamer leg.; D.B. Baker det. 1985; NHMUK • 2♂; Hatta (hotel); 7 Nov. 1986; I.L. Hamer leg.; D.B. Baker det. 1985; NHMUK • 2♂; Jebel Ali [Mina Jebel Ali]; 25 Oct. 1991; I.L. Hamer leg.; D.B. Baker det. 1992; NHMUK • 1♂, 1♀; Shweib/Suweihan [Sweihan]; 12 Feb. 1987; I.L. Hamer leg.; D.B. Baker det. 1987; NHMUK; **Yemen** • 1♂; W. Aden Protect., Wadi Tiban [Wadi Tuban], N.W. of Jebel Jihaf; ca. 3800 ft. a.s.l.; 21 Oct. 1937; H. Scott and E.B. Britton leg.; NHMUK (***holotype***) • 1♂; Lahej [Lahij], Arabia; 20 Feb. 1895; C.G. Nurse leg.; M.A. Lieftinck 1967 det.; RMNH; RMNH.INS.1714261 (***paratype***)

Figure 8. *Thyreus nadigi* (Alfken, 1933) male holotype (ZMHB). **A.** Label details; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Scutum, dorsal view; **E.** Metasoma, dorsal view; **F.** Metasoma, dorsal view detail.

• 1♂; Lakej-Aden; 12 Feb. 1895; C.T. Bingham leg.; M.A. Lieftinck det.; ZMHB (***paratype***).

Notes. Lieftinck (1968) described *T. parthenope* with a *locus typicus* in southern Yemen, approximately 100 km north of Aden. Lieftinck described only the male sex, with most specimens known from Yemen and one additional specimen from Egypt (precise location within Egypt unknown). Examination of additional material collected after 1968 shows that *T. parthenope* has a wider distribution across the southern half of the Arabian Peninsula, being found also in Saudi Arabia, the United Arab Emirates, and Oman. An additional Egyptian specimen was located (NHMW), but it also lacked precise collecting details. Most of the other museum specimens were identified by Donald Baker in the 1980s and 1990s, but details were never published, and Baker never described the unknown female that was captured flying with the male in the United Arab Emirates.

Diagnosis. Lieftinck (1968: 112) indicated that the female is likely to be recognised by one shared character with the male, which is the presence of two distinct white hair spots on the scutum. The female specimen

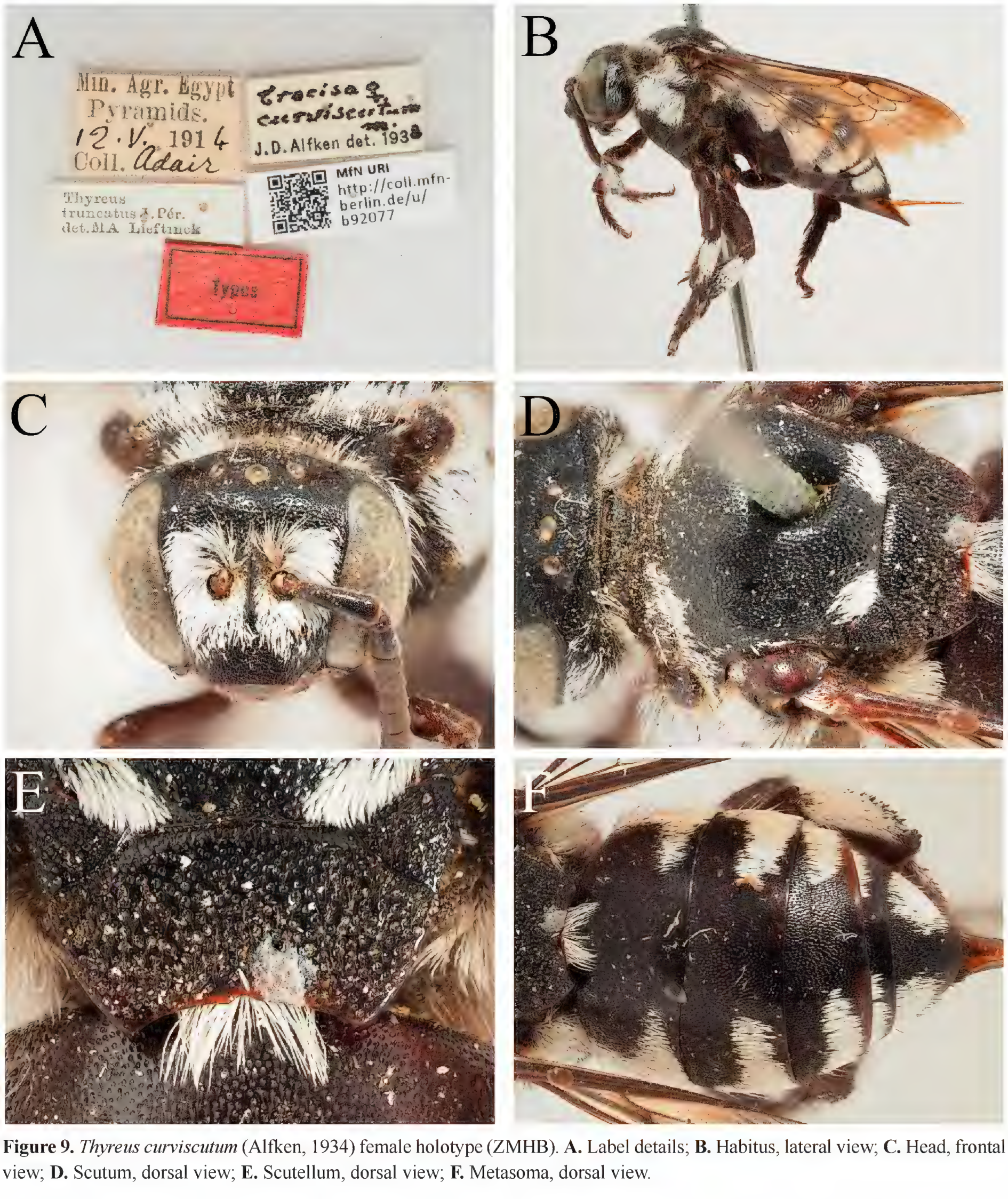

Figure 9. *Thyreus curviscutum* (Alfken, 1934) female holotype (ZMHB). **A.** Label details; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Scutum, dorsal view; **E.** Scutellum, dorsal view; **F.** Metasoma, dorsal view.

captured with the male *T. parthenope* in Sweihan (United Arab Emirates, see examined material below) displays this character (Fig. 11E) and also shows additional characters that allow separation from similar species. It can be recognised due to the presence of an unbroken line of white hairs running along the entire length of the lateral margins of the scutum (Fig. 11D), as in *T. priesneri* Lieftinck, 1968 (see below), *T. ramosus* (Lepeletier, 1841), and *T. ramosellus* Cockerell, 1919 (in *T. histrionicus* with the scutum laterally with some dark hairs, never with a complete unbroken line of white hairs). Separation from *T. priesneri*, *T. ramosus*, and *T. ramosellus* can be made by the presence of distinct white hair patches on the scutellum (Fig. 11E; without such patches in the three comparison species), and also because the axillae are covered with a dense tuft of adpressed white hairs (Fig. 11E), whereas in the comparison species the axillae lack such hair patches (being entirely black haired). *Thyreus priesneri* can also be separated due to the structure of the pygidial plate, which is flat and irregularly punctate, whereas in *T. parthenope* the pygidial plate is impunctate has a longitudinal bump or ridge medially.

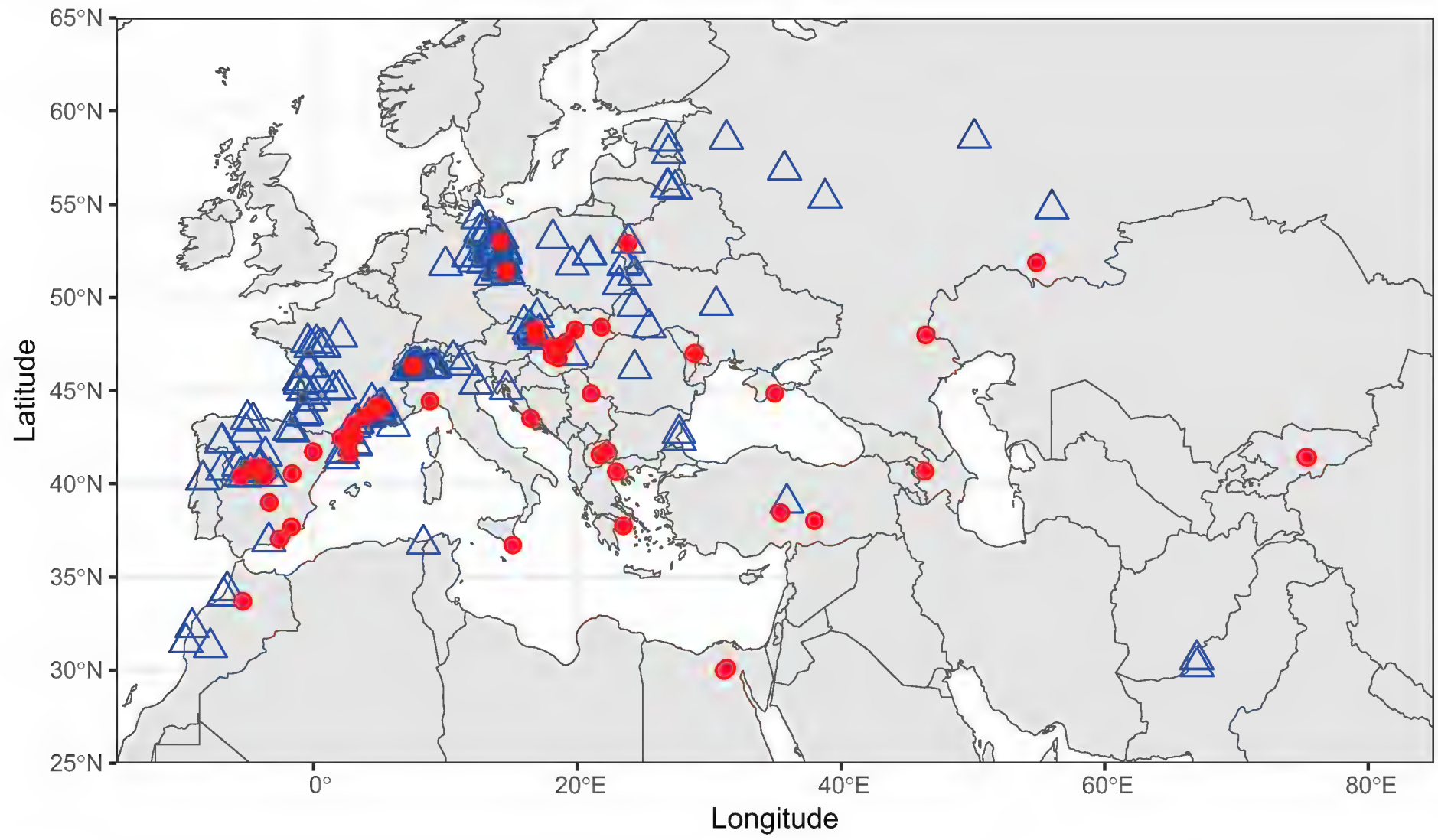

Figure 10. Distribution of *Thyreus truncatus* (Pérez, 1884) (red circles) along with its host *Tetralonia dentata* (Germar, 1839) (open blue triangles). Distributional data are not comprehensive.

The presence of white hair patches on the axillae gives *T. parthenope* a similar appearance to *T. hyalinatus* (Vachal, 1903) (Israel, Egypt, Sudan, Chad*, Eritrea, Djibouti, Saudi Arabia, Qatar*, United Arab Emirates*, Oman*, Iran; Lieftinck 1968), but the two species can be separated by the presence of the white hair spots on the scutellum of *T. parthenope* (absent in *T. hyalinatus*). The two species can also be separated due to the structure of the mesepisternum in its ventral half (the part not covered with pubescence), which has the punctures dense and very weakly separated in *T. parthenope* (punctures almost confluent), whereas *T. hyalinatus* shows clear shining spaces between the punctures, these spaces often wider than the diameter of a puncture. These characters, in combination with the distribution, which is currently restricted to the southern half of the Arabian Peninsula and probably south-eastern Egypt allows recognition, particularly in combination with concurrently active males.

Description. Female. Body length: 12 mm (Fig. 11A). ***Head*:** Dark, 1.3 times wider than long (Fig. 11B). Clypeus very weakly domed, densely punctate, punctures separated by ≤ 0.5 puncture diameters, interspaces shining. Labrum rounded rectangular, 1.5 times longer than broad, with longitudinal impressed midline terminating subapically, apex with tiny slightly projecting tooth; labrum basally strongly produced into two tubercles laterally, outer half of tubercules polished and shining, impunctate. Gena much narrower than width of compound eye; ocelloccipital distance 2 times diameter of lateral ocellus. Face between antennal insertions with weakly raised longitudinal carina, not strongly extending dorsally. Frons densely punctate, punctures separated by ≤ 0.5 puncture diameters, becoming weaker laterally adjacent to lateral ocelli, here with polished shining impunctate space subequal to diameter of lateral ocellus (Fig. 11C). Head almost entirely white-haired, with brownish hairs restricted to mandibles. Antenna dark, measured along ventral surface A3, more or less equalling A4.

***Mesosoma*:** Scutum and scutellum densely punctate, punctures separated by ≤ 0.5 puncture diameters, up to 1 puncture diameter on scutellum, surface between punctures shiny. Scutum with contrasting black and white pubescence, white pubescence along anterior margin, lateral margins, medially with longitudinal line covering anterior ¾ of scutum, anterolaterally with two white spots, posterolaterally with two thick patches along posterior margin (Fig. 11D). Axilla with clear patch of white plumose adpressed hairs. Scutellum postero-laterally with two patches of white plumose adpressed hairs. Scutellum produced into two posteriorly projecting points, between these with shallow emargination, scutellum itself relatively long, maximum width 1.5 times longer than maximum length; emargination between posterior points with thick broad tuft of white hairs emerging from ventral surface (Fig. 11E). Mesepisternum in dorsal ½ covered with dense patch of adpressed white hairs, entirely obscuring surface; in ventral ½ with surface lacking hairs, densely and regularly punctate, punctures almost confluent. Legs dark, outer surface of tibiae and tarsi covered with dense felt-like white hairs, mid and hind tibiae with short dark spines projecting through pubescence. Forewing almost entirely hyaline, with only weak infuscation adjacent to a few veins.

***Metasoma*:** Terga dark, tergal discs densely punctate with hair-bearing punctures, punctures presenting

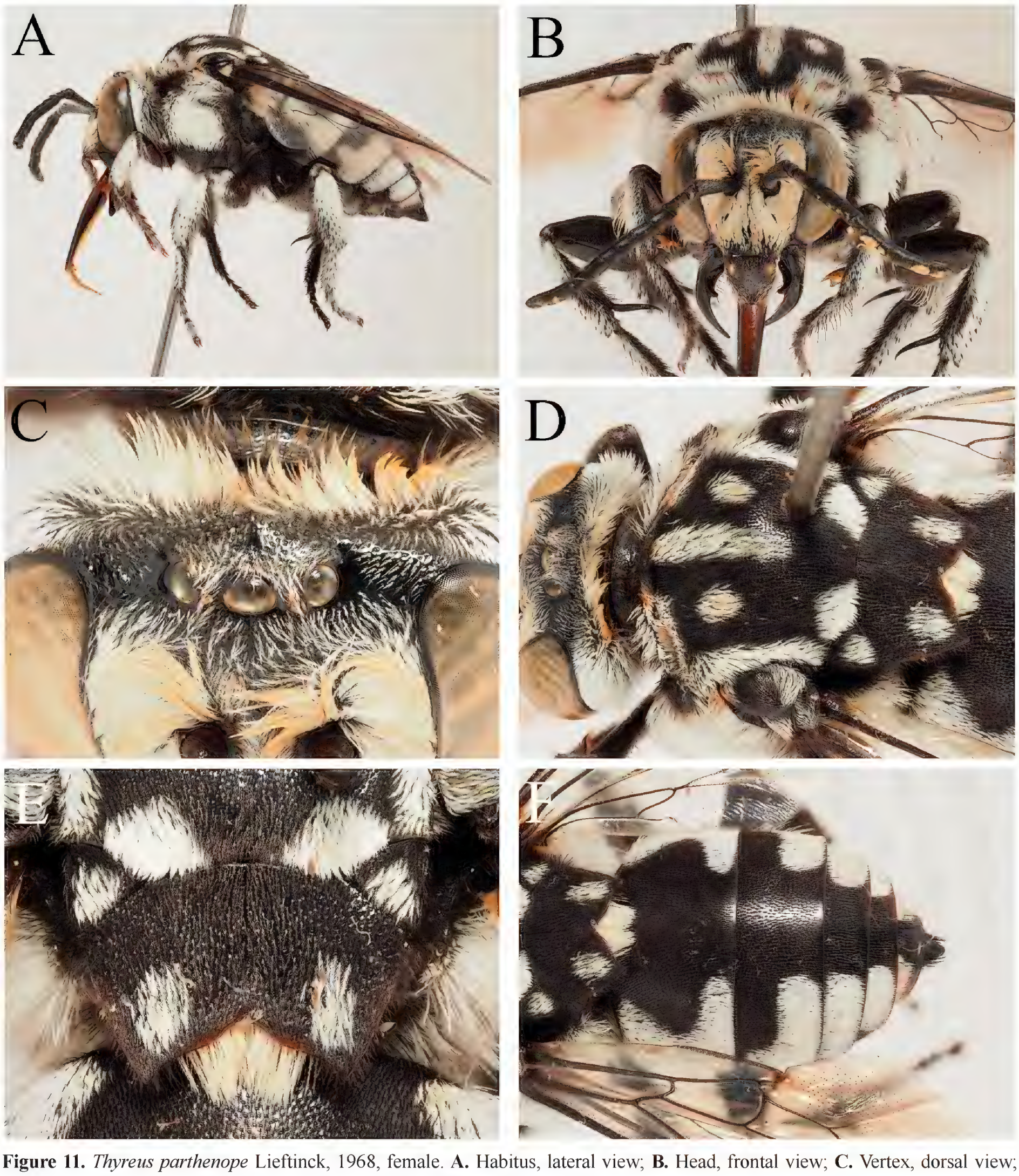

Figure 11. *Thyreus parthenope* Lieftinck, 1968, female. **A.** Habitus, lateral view; **B.** Head, frontal view; **C.** Vertex, dorsal view; **D.** Scutum, dorsal view; **E.** Scutellum, dorsal view; **F.** Metasoma, dorsal view.

short, posteriorly projecting black plumose hairs, punctures separated by 0.5–2 puncture diameters (Fig. 11F). T1 laterally with wide C-shaped patch of white hairs, hairs along apical margin of tergum reaching further towards centre of disc than hairs along basal margin of tergum. T2 with L-shaped patch of white hairs, T3–5 with rectangular white hair patches, hair patches on all terga broadly separated medially, never complete. Pygidial plate weakly converging apically, lateral margins slightly raised, medially with strongly humped longitudinal bump, surface dull.

Distribution. Egypt (presumably southern Egypt), Sudan*, Saudi Arabia*, Yemen, United Arab Emirates*, Oman* (Lieftinck 1968).

Other material examined. (*Thyreus hyalinatus*) **Chad** • 1♀; Tchad, Ndjamena; 30 Mar. 1978; G.G.M. Schulten leg.; RMNH • 1♀; Tchad, Ndjamena; 22 Jun. – 6 Jul. 1978; G.G.M. Schulten leg.; RMNH; **Oman** • 2♀; 20 km W Barka, Wadi Far; 14 Mar. 2022; C. Schmid-Egger leg.; CSE • 6♂, 1♀; Dhaufur, Thumrait 35 km N, KF desert farm; 21 Sep. 2023; C. Schmid-Egger & W-H. Liebig leg.; CSE/TJWC/WHLC • 1♂; Dhofar, 2 km W Taqah; 29 Aug. 2019;

C. Schmid-Egger leg.; CSE • 1♀; Dhofar, 35 km N Thumrait, Najd; 3 Sep. 2019; C. Schmid-Egger leg.; CSE • 1♀; SW of Sur; 3–5 Mar. 2017; M. Snižek leg.; OÖLM; **Qatar** • 1♂; Al Shahaniyeh [Ash-Shahaniyah]; 9 May 1980; C.G. Roche leg.; D.B. Baker det. 1993; OUMNH • 1♂; Al Shahaniyeh [Ash-Shahaniyah]; 23 May 1980; C.G. Roche leg.; D.B. Baker det. 1993; OUMNH • 5♂; Al Shahaniyeh [Ash-Shahaniyah]; 13 Jun. 1980; C.G. Roche leg.; D.B. Baker det. 1993; OUMNH; **United Arab Emirates** • 1♀; Wadi Bih, dam; 29 Nov. 2009; A. van Harten leg.; CSE.

Thyreus picaron Lieftinck, 1968

Thyreus picaron Lieftinck, 1968: 92, ♂ [Croatia, RMNH, examined].

Material examined. **Albania** • 1♂; Topovë; 13 Jul. 2017; K. Janssen leg.; KJCB; **Bulgaria** • 1♂; Melnik; 4 Jul. 2019; M. Halada leg.; OÖLM; **Croatia** • 1♂; Stobreč (nr. Split); 13 Jun. 1962; C. v. Heijningen leg.; M.A. Lieftinck det.; RMNH; RMNH.INS.1714262 (***holotype***) • 1♂; Baška, Insel Krk; 16 Aug. 1976; J. Heinrich leg.; OÖLM; **Cyprus** • 1♂; 20 km NNW Pafos, Lara Beach; 20 Jun. 2013; C. Schmid-Egger leg.; CSE • 1♂; Akrotiri; 26 Apr. 2018; A. Varnava leg.; TJWC; **France** • 1♂; Alpes Maritimes, 1 km S Fontan; 13 Jul. 2009; C. Schmid-Egger leg.; CSE • 1♂; Var, Le Trayas; O.W. Richards leg.; M.A. Lieftinck det.; NHMUK; **Georgia** • 1♂; Tbilissi, Botanical Garden; 26 Jul. 2021; V. Leclercq leg.; E. Dufrêne det., VLC; **Greece** • 1♂; Chalkidiki, W of Nikiti; 12–14 Jun. 2013; M. Snižek leg.; OÖLM • 1♂; Karpenission, 2000 ft [Karpenisi]; 20 Jul. 1976; K.M. Guichard leg.; M.A. Lieftinck det.; NHMUK • 1♂; Preveza env.; 25 Jun. 1997; K. Deneš leg.; OÖLM; **Iran** • 1♂; Golestan, Kashidar; 1381 m a.s.l.; 9 Jul. 2018; W-H. Liebig leg.; WHLC • 1♂; Semnan province, Shahmirzad, 13 km NW; 1836 m a.s.l.; 7 Jul. 2022; C. Schmid-Egger leg.; CSE • 1♂; Teheran province, Elburz, Serkheh [Sorkheh Zamin]; 2266 m a.s.l.; 6 Jul. 2022; C. Schmid-Egger leg.; CSE • 1♀; Tehran prov., Elburz, Firuzkuh 1 km SW; 6 Jul. 2022; C. Schmid-Egger leg.; CSE; **Italy** • 1♂; S-Tirol, Meran, Schloss-Trauttmansdorf; 21 Aug. 2013; T. Kopf leg.; CSE • 1♂; S-Tirol, Meran, Schloss-Trauttmansdorf; 11 Aug. 2013; T. Kopf leg.; CSE; **Lebanon** • 1♂; Nord Libanon, Becharre [Bsharri]; 1400 m a.s.l.; 1–4 Jul. 1931; Zerny leg.; M.A. Lieftinck det.; RMNH; RMNH.INS.1714263; **Montenegro** • 1♂; Ulcinj; 29 Jun. 1969; Hoffer leg.; OÖLM; **North Macedonia** • 1♂; Suvodol, 18 km ENE of Bitola; 750–1000 m a.s.l.; 30 Jul. 1965; M.A. Lieftinck det.; RMNH; RMNH.INS.1714264; **Romania** • 1♂; Dobrogea [remaining text illegible]; 7 Jul. 1994; OÖLM; **Slovakia** • 1♂; Sturovo [Štúrovo]; 28 Jul. 1972; M. Kocourek leg.; OÖLM; **Spain** • 1♂; Catalonia, Palamos; 19 Jul. 1959; S.G. Bishoff leg.; M.A. Lieftinck det.; ZMHB • 1♂; N. of Madrid, Rio Guadarrama; 27 Jul. 1980; K.M. Guichard leg.; NHMUK • 1♂; Segovia, Brieva, 5 km N, Las Cañones de los rios Piron y Viego; 16 Jul. 2021; T.J. Wood leg.; TJWC • 1♂; Valencia; [undated]; Moroder leg.; MNCN • 1♂; Pontevedra, Cortellas; [undated]; Varela leg.; MNCN; **Turkey** • 1♂; Bitlis, Nemrut Dağı; 2300 m a.s.l.; 15 Aug. 1991; J. Halada leg.; OÖLM; **Ukraine** • 1♂; Odessa [Odesa] Oblast, Krasnosilka env.; 23 Jun. 2024; A.V. Gontarenko leg.; E. Dufrêne det., VLC.

Remarks. It was possible to identify the female of *T. picaron* through DNA barcoding. Unfortunately, the located female from Iran (WPATW1024-23) appears to be completely identical to *T. histrionicus* (Panzer, 1806). It therefore does not currently seem possible to provide a diagnosis for the female sex, and so future records of *T. histrionicus* from within the expanded distributional range (relative to Lieftinck 1968) of *T. picaron* must be considered in a broad sense. Examination of additional material has increased the distributional range of *T. picaron*, particularly in south-eastern Europe (Fig. 12). As suggested by Gaspar et al. (2025), the host is likely to be one or both of two of the larger *Amegilla* sensu stricto, either *Am.* (*Amegilla*) *garrula* (Rossi, 1790) or *Am.* (*Amegilla*) *ochroleuca* (Pérez, 1879). Like these two possible

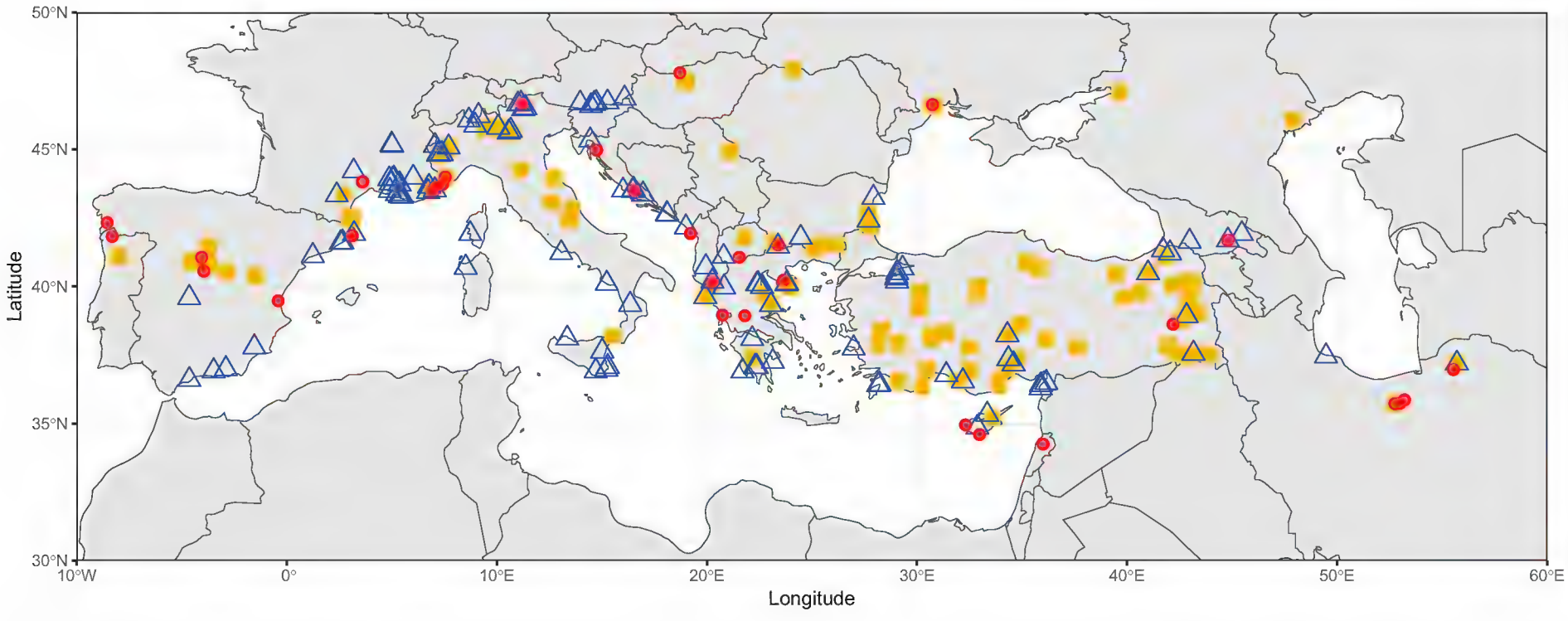

Figure 12. Distribution of *Thyreus picaron* Lieftinck, 1968 (red circles) along with its two suspected hosts, *Amegilla garrula* (Rossi, 1790) (open blue triangles) and *Amegilla ochroleuca* (Pérez, 1879) (filled yellow squares). Distributional data are not comprehensive.

hosts, *T. picaron* does not extend into North Africa. Records of *Am. garrula* and *Am. ochroleuca* are presented in Suppl. material 1. The use of two hosts is suspected due to areas where only one possible host is known (with a high degree of confidence) to be present, such as in central Spain and northern Portugal (*Am. garrula* absent) and northernmost Italy (*Am. ochroleuca* absent). At the Italian sites surveyed in 2013, *T. picaron* was flying with *Am. garrula*, supporting this association. *Thyreus picaron* has also been regularly collected with *Am. garrula* in the south of France (M. Aubert, pers. comm.).

Based on this hypothesis, *T. picaron* should be common in Turkey; a study of additional Turkish *Thyreus* specimens to clarify its range in this country is necessary. It is important to note that there is a cryptic species close to *Am. ochroleuca* which is currently being described from Lebanon, eastern Turkey (Ağrı, Hakkâri), northern Iran, and south-western Turkmenistan (P. Rasmont & TJW, in preparation); it is very rare in collections and is collected much more rarely than *Am. ochroleuca* in Turkey. It may serve as a third host species for *T. picaron*. For simplicity, these records are here folded into *Am. ochroleuca*. In northern Iran, *T. picaron*, the cryptic "*Am. ochroleuca*", and *Am. garrula* have all been caught in close proximity (Fig. 12). We report *T. picaron* as new for the fauna of Ukraine, from where *Am. ochroleuca* has also been recorded (see Suppl. material 1), and this species is also known from the Odesa region based on specimens held in the Kansas collection and determined by Brooks (KSEM1323579; Ascher and Pickering 2025), providing a plausible host. We also report *T. picaron* as new for Georgia, at a collecting locality where several *Am. garrula* were also captured (see Suppl. material 1).

Distribution. Portugal, Spain, France, Italy, Austria, Slovakia*, Slovenia, Croatia, Serbia, Romania, Ukraine*, Montenegro*, Albania*, North Macedonia, Bulgaria, Greece, Cyprus, Turkey, Georgia*, Lebanon*, Iran (Lieftinck 1968 *partim*; Kuhlmann et al. 2014; Varnava et al. 2020; Ascher and Pickering 2025; Gaspar et al. 2025; Fig. 12). As discussed above, we suspect that records from Central Asia will correspond to *T. jansseni*.

Thyreus priesneri Lieftinck, 1968

Thyreus priesneri Lieftinck, 1968: 124, ♂ [Egypt, type location unclear].

Material examined. Saudi Arabia • 1♂, 1♀; Abu Arish; 25 Mar. 1980; K.M. Guichard leg.; D.B. Baker det. 1981; NHMUK.

Notes. Lieftinck (1968) described *T. priesneri* from a single male specimen collected from southern Egypt (Gebel Elba). This specimen was cited as being in the collection of Hermann Priesner at "Linz", but it could not be located there, and its current deposition is therefore not immediately clear; further study is required to trace it. Fortunately, the description is well illustrated, allowing confident recognition. In the NHMUK collection, two specimens from Saudi Arabia were found; as with *T. parthenope*, these specimens were identified by Baker but were never published. The male clearly matches the criteria identified by Lieftinck, and due to co-occurrence and close morphology, the female can now be recognised (Fig. 13). The female can be diagnosed based on a combination of characters, but care must be taken, as they are quite subtle. The clearest confusion is with *Thyreus fallibilis* (Kohl, 1905), which was described from southern Yemen (Fig. 14). Lieftinck (1968) diagnosed this species and described the unknown male; due to the similarity of the females, this species is diagnosed last.

Diagnosis. As in *T. parthenope*, *T. priesneri* has an unbroken line of white hairs running along the entire length of the lateral margins of the scutum (Fig. 13E), as in *T. ramosus* (Lepeletier, 1841) and *T. ramosellus* Cockerell, 1919. *Thyreus parthenope* is diagnosed above, displaying white hair patches on the axillae and scutellum, whereas these areas are black-haired in *T. priesneri* (Fig. 13E), which also shows the lower half of the mesepisternum with large shining interspaces (Fig. 13D; with some interspaces reaching 3 puncture diameters), whereas in *T. parthenope* this area is densely punctate, without large shining interspaces. This shining and sparsely punctate mesepisternum also allows separation from *T. ramosus* and *T. ramosellus*, and indeed it is strange that Lieftinck diagnosed *T. priesneri* against *T. ramosus* when in the construction of the genital capsule and the shining lower half of the mesepisternum it is much closer to *T. hyalinatus* (Vachal, 1903), with which it has an overlapping range in Egypt and the Arabian Peninsula. *Thyreus priesneri* can be differentiated from the latter species due to the axillae with black hairs (Fig. 13E; in *T. hyalinatus* with white patches of hairs covering the axillae), the L-shaped patches of hairs on the lateral parts of T1 (Fig. 13F), these being uneven, with the apical part projecting further towards the centre of the tergal disc than the basal part (in *T. hyalinatus* with the C-shaped patches of hairs more even, with both the basal and apical parts uniformly projecting towards the centre of the tergal disc), and the posterior margin of the scutellum, which has posteriorly projecting white hairs emerging from below but not sitting on the dorsal side of the disc (Fig. 13E; in *T. hyalinatus* with hairs emerging both from below the posterior margin of the scutellum and present on the dorsal side of the posterior margin of the disc). This combination of characters (continuous line of white hairs on the lateral margins of the scutum, lower half of the mesepisternum sparsely punctate with large shining interspaces, and axillae and scutellum entirely black-haired) should allow recognition of females of *T. priesneri* compared to other species in north-eastern Africa and the Arabian Peninsula.

For diagnosis against *T. fallibilis*, the overall pubescence pattern is highly similar, as well as the punctation and microsculpture of the integument, such as in the lower part of the mesepisternum with large shining interspaces (Fig. 14D), the vertex domed in frontal view (Fig. 14C), and the scutellum of similar shape and with

Figure 13. *Thyreus priesneri* Lieftinck, 1968, female. **A.** Habitus, lateral view; **B.** Head, frontal view; **C.** Labrum, ventral view; **D.** Mesepisternum, ventrolateral view; **E.** Scutum, dorsal view; **F.** Metasoma, dorsal view.

similar puncture density (Fig. 14E). The key difference is in the structure of the individual hairs; in *T. fallibilis*, the hairs are flattened and strongly plumose, with the branches spreading laterally, becoming almost scale-like (Fig. 14E, F). In *T. priesneri*, the hairs are plumose but are not flattened, and the branches do not spread laterally, meaning that they have a more quill-like appearance (Fig. 13E, F). This can be seen most clearly on the disc of T1. As noted by Lieftinck (1968: 96), the pubescence of *T. fallibilis* is also slightly tinted with blue, whereas in *T. priesneri* the pubescence is pure white. We maintain the species concepts presented by Lieftinck, but this putative species pair would benefit from molecular investigation.

Description. Female. Body length: 9 mm (Fig. 13A). ***Head*:** Dark, 1.2 times wider than long (Fig. 13B). Clypeus slightly elevated, more or less flattened across disc, densely punctate, punctures separated by ≤ 0.5 puncture diameters, interspaces shining. Labrum broadly rounded rectangular, lateral margins converging, apex thus narrower than base, labrum only slightly longer than basal width. Labrum basally with two slightly raised tubercules, medially with impressed furrow, this terminating

Figure 14. *Thyreus fallibilis* (Kohl, 1905) holotype female. **A.** Label details; **B.** Habitus, lateral view; **C.** Face, frontal view; **D.** Mesepisternum, lateral view; **E.** Scutum, dorsolateral view; **F.** Metasoma, dorsal view.

subapically at strong transverse carinae, medially produced into pointed tooth (Fig. 13C). Gena much narrower than width of compound eye, posteriorly with strongly raised winged carinae, narrowing to be almost imperceptible along posterior margin of vertex; ocelloccipital distance 1.5 times diameter of lateral ocellus. Face between antennal insertions with weakly raised longitudinal carina, not strongly extending dorsally. Frons densely punctate, punctures separated by 0.5–1 puncture diameters, with slight impunctate space adjacent to lateral ocelli, space subequal to diameter of lateral ocellus. Head almost entirely white-haired, with brownish hairs restricted to mandibles. Antenna dark, measured along ventral surface A3, slightly but distinctly shorter than A4.

***Mesosoma*:** Scutum and scutellum densely punctate, punctures somewhat irregular, separated by < 0.5–1 puncture diameters, punctures most consistently dense on scutellum, surface shiny. Scutum with contrasting black and white pubescence, abundant white pubescence along anterior margin, lateral margins, medially with longitudinal line covering anterior ½ of segment, anterio-laterally with two white spots, postero-laterally with two thick patches

along posterior margin (Fig. 13E). Axillae and scutellum entirely black haired on dorsal surface. Scutellum produced into two posteriorly projecting points, between these with shallow emargination, scutellum itself relatively long, maximum width 1.5 times longer than maximum length (measured from base to midpoint between posterior points); emargination between posterior points with thick broad tuft of white hairs emerging from ventral surface.

Mesepisternum in dorsal ½ covered with dense patch of adpressed white hairs, entirely obscuring surface; in ventral ½ with surface lacking hairs, with split punctation; in anterior portion with surface abundantly punctate, punctures separated by < 0.5–1, in posterior portion with punctures becoming very sparse, punctures separated by 1–4 puncture diameters, interspaces smooth and polished (Fig. 13D). Legs dark, outer surface of tibiae covered with dense felt-like white hairs, mid and hind tibiae with short dark spines projecting through pubescence. Forewing with varied colouration, predominantly hyaline with infuscation adjacent to vein, within submarginal and marginal cells, and on apical papillate region.

***Metasoma*:** Terga dark, tergal discs densely punctate with hair-bearing punctures, punctures presenting short, posteriorly projecting black plumose hairs, punctures separated by 0.5–2 puncture diameters, extending onto majority of marginal areas, with marginal areas narrowly impunctate along apical rim (Fig. 13F). T1 laterally with large patch of white hairs, these not typically C-shaped, more L-shaped with apical part projecting further towards centre of disc than basal part. T2 with broad L-shaped patch of white hairs, T3–5 with rectangular white hair patches, hair patches on all terga broadly separated medially, never complete. Pygidial plate long, triangular, narrowly rounded, lateral margins slightly raised, surface flat, irregularly punctate with punctures of variable sizes, surface very obscurely shining.

Distribution. Southern Egypt and Saudi Arabia* (Lieftinck 1968).

Other material examined. (*Thyreus fallibilis* (Kohl, 1905)) **Yemen** • 1♀; Makalla [Al Mukalla]; 1–30 Apr. 1899; O. Simony leg.; NHMW (***holotype***).

New distributional data and range clarifications

Thyreus hellenicus Lieftinck, 1968

Thyreus hellenicus Lieftinck, 1968: 71, ♀♂ [Greece, RMNH, examined] (Fig. 15A–D).

Material examined. **Greece** • 1♂; Parnass[us]; 19 Jul. 1956; Bytinski-Salz leg.; M.A. Lieftinck det.; RMNH; RMNH.INS.1714335 (***holotype***) • 1♂; Parnass[us]; 19 Jul. 1956; Bytinski-Salz leg.; M.A. Lieftinck det.; RMNH; RMNH.INS.1662710 (***paratype***) • 1♀; Graecia, Peloponnesus, Alt-Korinth; 3 Jun. 1964; M. Schwarz leg.; M.A. Lieftinck det.; RMNH; RMNH.INS.1662711 (***paratype***) • 1♀; I. Kalymnos, Pothia; 2–4 Jun. 1935; O. Wettstein; NHMW • 1♂; Legrena; 1 Jun. 1965; K.V. Krombein leg.; M.A. Lieftinck det.; RMNH; RMNH.INS.1662712 (***paratype***) • 3♀; Amorgos, Agioi Saranta; 1 m a.s.l.; 19 Jun. 2023; V. Leclercq leg.; V. Leclercq det.; VLC/EDC • 1♂; Gythion [Gytheio]; 3 Jun. 1937; F. Werner leg.; NHMW (***paratype***); **Kazakhstan** • 2♂; Uralsk; M. Bartel leg.; NHMW (***paratypes***); **Spain** • 1♂; Madrid [no further information]; G. Mercet collection; MNCN; MNCN_Ent 436609; (***paratype***); **Syria** • 1♂; S. Syria: Mount Hermon; 30 Jul. 1945; G.H. Q. & M.E.F. leg.; M.A. Lieftinck det.; NHMUK (***paratype***); **Turkey** • 1♂; Cankiri, 15 kms Ilgaz-Cankiri Rd.; 1400 m a.s.l.; 23 Jul. 1962; Guichard & Harvey leg.; M.A. Lieftinck det.; NHMUK (***paratype***) • 1♂; Cankiri, 15 kms Ilgaz-Cankiri Rd.; 1400 m a.s.l.; 23 Jul. 1962; Guichard & Harvey leg.; M.A. Lieftinck det.; RMNH; RMNH.INS.1714265 (***paratype***) • 1♂, 1♀; Konya, Sultan Dağları, 10 km S of Çay; 1300 m a.s.l.; 18–25 Jul. 1980; H. v. Oorschot leg.; RMNH; ZMA.INS.5144951.

Notes. *Thyreus hellenicus* is a poorly known species most commonly encountered in the East Mediterranean. Lieftinck (1968: 76) imprecisely stated "the Whole Mediterranean region" when discussing the distribution, despite presenting specimens from only Spain, Greece, Turkey, Syria, and north-western Kazakhstan (the southern tip of the Ural Mountains). Discussion of the range of this species combined with its host is necessary.

Thyreus hellenicus was described from Mount Parnassus in southern Greece, and most specimen records presented by Lieftinck were from this country. Specimens from Greece, Turkey, and Syria (Mount Hermon) are morphologically consistent and recognisable (see characters in the identification key below). It was possible to examine the paratype from Spain (MNCN) from the collection of Ricardo García Mercet (Fig. 16). It has been dissected and is indeed *T. hellenicus* based on the size and genital capsule (Fig. 16D), as indicated by Lieftinck. The presence of this species in Spain remains perplexing, but we suggest that it may be plausible with some caveats (see below concerning host use). The two specimens from Uralsk (NHMW) are morphologically consistent with *T. hellenicus*; they were not actually labelled as *T. hellenicus* by Lieftinck and bore labels of "*Thyreus praevalens* det. M.A. Lieftinck" with no date, but they are clearly the specimens to which he was referring in his 1968 publication. Paratype labels have been added. The presence of *T. hellenicus* in western Kazakhstan is possible if broad host use of *Anthophora* bees of the subgenus *Paramegilla* Friese, 1897, is the life-history choice of this parasite (see below). Finally, we believe that Lieftinck's comments that *T. hellenicus* could be present in Romania (based on the genital illustrations of *T. histrionicus* presented by Iuga 1958: 214) are unjustified. The genital capsule illustrated by Iuga has the gonostylus small, slender, and sparsely haired, suggesting a member of the *scutellaris*-group. We therefore consider the presence of *T. hellenicus* in Romania to be implausible based on the currently available evidence, including revision of *Thyreus* material from northern Greece and Bulgaria.

Figure 15. *Thyreus hellenicus* Lieftinck, 1968 holotype male (RMNH). **A.** Label details; **B.** Habitus, lateral view; **C.** Face, frontal view; **D.** Metasoma, dorsal view; Paratype male (RMNH); **E.** Genital capsule, dorsal view; **F.** Genital capsule, lateral view.

In addition, based on new observations on the island of Amorgos, we can demonstrate that at least one of the hosts of *T. hellenicus* is *Anthophora* (*Paramegilla*) *superans* Walker, 1871. On 19 June 2023, in a bare, sandy area of the preserved beach of Agioi Saranta on the island of Amorgos, Greece, one of us (VL) observed three females of *T. hellenicus* flying in and out of nests located in the ground, with simultaneous visitation of the same nests by *Anthophora* females, specifically *Anthophora* (*Paramegilla*) *superans*. Moreover, *An. superans* was the only large anthophorine bee of the same size as *T. hellenicus* present at the collecting event (and possibly even on the island of Amorgos) at this time. Further support for this association is the paratype of *T. hellenicus* collected by Max Schwarz at Corinth on 3 June 1964; he also collected a long series of *An. superans* at the same moment (specimens OÖLM/TJWC; see Suppl. material 1). The same can be said for the paratype from Gytheio on 3 June 1937 (NHMW), which was also collected with several *An. superans* (specimens NHMW).

The name of the *Anthophora* host requires explanation, as this name has not previously been used for the

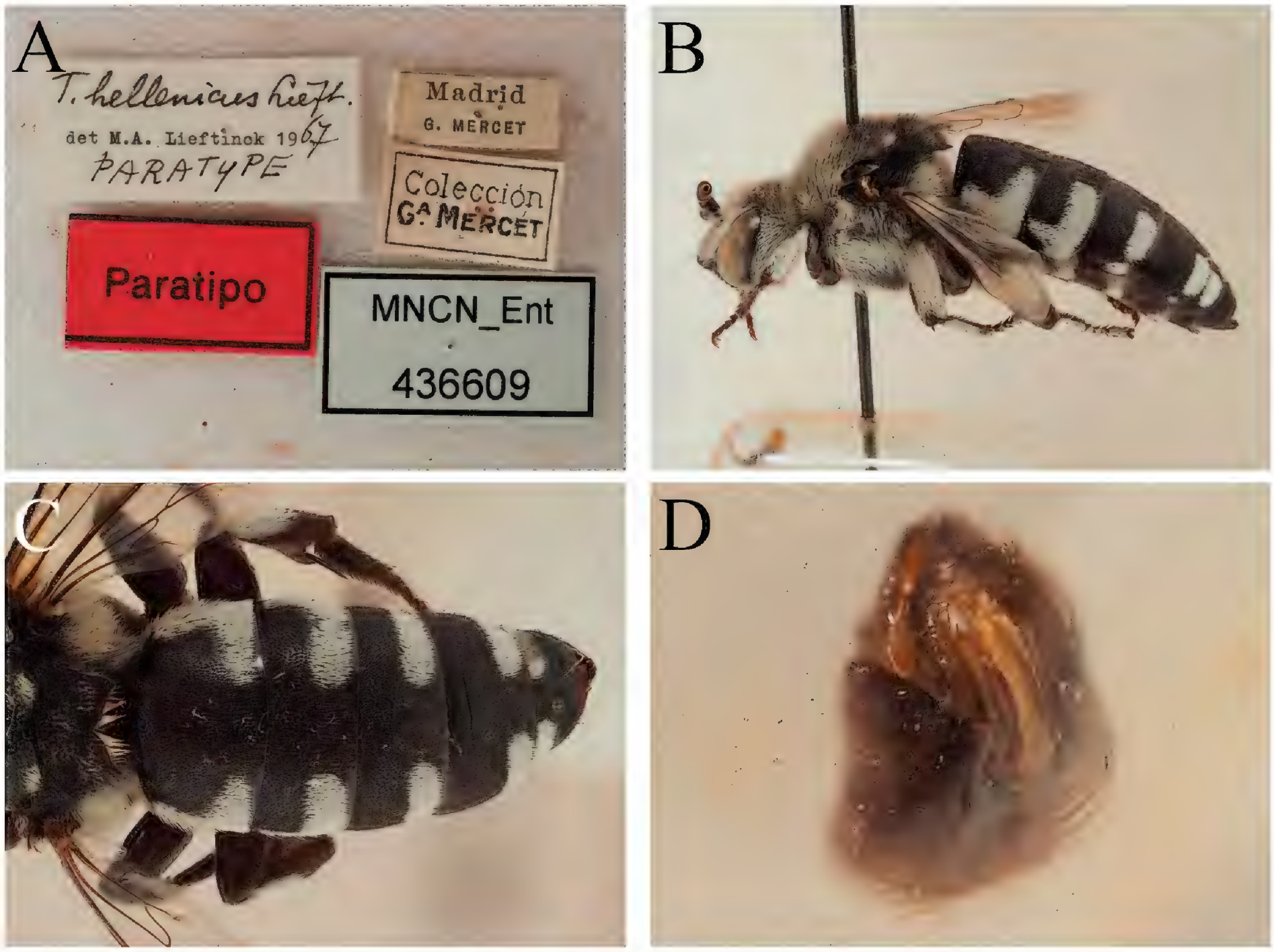

Figure 16. *Thyreus hellenicus* Lieftinck, 1968 paratype male (MNCN). **A.** Label details; **B.** Profile; **C.** Metasoma, dorsal view; **D.** Genital capsule, dorsal view.

European fauna. The presence of a large *Paramegilla* species in southern and Aegean Greece has been known for a long time; Dours (1869: 120) used the name *Anthophora dubia* Eversmann, 1852, giving a distribution of "Îles de l'Archipel grec, montagnes de l'Oural, province d'Orenbourg, d'après Eversman". The identity of *An. dubia* is currently being dealt with elsewhere (Rasmont et al., *in review*), but in short, *An. dubia* was described from Orenburg in southern European Russia and comprises a mixed type series (males and females incorrectly associated). Neither taxon within this type series is conspecific with the Greek bee, which is an East Mediterranean species. Searches were therefore made for the appropriate name to apply to this large and conspicuous *Anthophora* species.

Examination of type material has concluded that the oldest names that can be applied are either *Anthophora* (*Paramegilla*) *inclyta* Walker, 1871, or *Anthophora* (*Paramegilla*) *superans* Walker, 1871. These two names come from Walker's (1871) work on Hymenoptera collected around the Red Sea in Egypt, Arabia, and Eritrea. Francis Walker (1809–1874) was a prolific worker who has been much criticised for his abundant and superficial descriptions; the lack of respect for the work of Walker by his contemporaries was clear at the time (see the 1874 obituary cited in Evenhuis 2008), a sentiment echoed by Baker (1993: 300), who commented on the case of *An. inclyta* and *An. superans*. Much of the material described in Walker (1871) has been lost (e.g. see Monks et al. 2024), but some specimens of *An. inclyta* and *An. superans* were preserved in the collection of Frederick Smith and are now held in the NHMUK (Baker 1993; see Other material examined, below).

Walker (1871: 58, no. 287) described *An. inclyta* in the female sex from "Rafla, Wady Ferran, Mount Sinai". This corresponds to Arafali/Irafayle in Eritrea, Wadi Feiran in Sinai, and Mount Sinai in the southern part of the Sinai Peninsula. He then (Walker 1871: 58, no. 288) described *An. superans* in the "female" sex from Mount Sinai only. In the NHMUK collection, there are 3♀ of *An. inclyta* and 4♂ of *An. superans*. Although Walker wrote "female" for *An. superans*, he described the head as "Head, excepting the vertex white and without hairs", suggesting a male, since the males have the clypeus, supraclypeal area, and lower paraocular areas with the integument yellow-white (Fig. 17C). It is therefore considered that *An. superans* was described from the male sex. A dissected male was labelled as "lectotype" by Baker in 1979 and by Brooks in 1983 (Fig. 17A), but neither of these designations was published. Although Baker (1993) wrote that it was designated as such, this was published in his PhD thesis, which does not meet the ICZN (1999) criteria for a valid

Figure 17. *Anthophora* (*Paramegilla*) *superans* Walker, 1871 lectotype male (NHMUK). **A.** Label details; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Hind leg, lateral view; **E.** Metasoma, dorsal view; **F.** Genital capsule, inverted along the transverse plane, lateral view.

publication. Under Articles 8 and 9, as the thesis was not a formally published work and only seven hard copies were produced, and these limited numbers were not obtainable either for free or for a charge, it fails Articles 8.1.2 and 8.1.3. This specimen from the Convent Garden on Mount Sinai (Saint Catherine's Monastery; 28.55°N, 33.98°E) is therefore finally published here as the lectotype of *An. superans*, by present designation. It is conspecific with the material from Greece based on the hind basitarsi, which have a rounded bump apically (Fig. 17D; no tooth or teeth), and based on the ventro-lateral projection of the gonocoxa, which is reduced (Fig. 17F; lectotype specimen with the genital capsule fixed in a capsule with a glycerine-like substance). This reduction in the lateral projection of the gonostylus allows separation from the West Mediterranean *Anthophora* (*Paramegilla*) *ferruginea* Lepeletier, 1841 (compare Fig. 18E, F). Indeed, the genital capsule is so similar (Fig. 18C, D) that Lieftinck treated material (RMNH) from the East Mediterranean as *An. ferruginea* ssp. *dubia*; these specimens have been re-determined (see

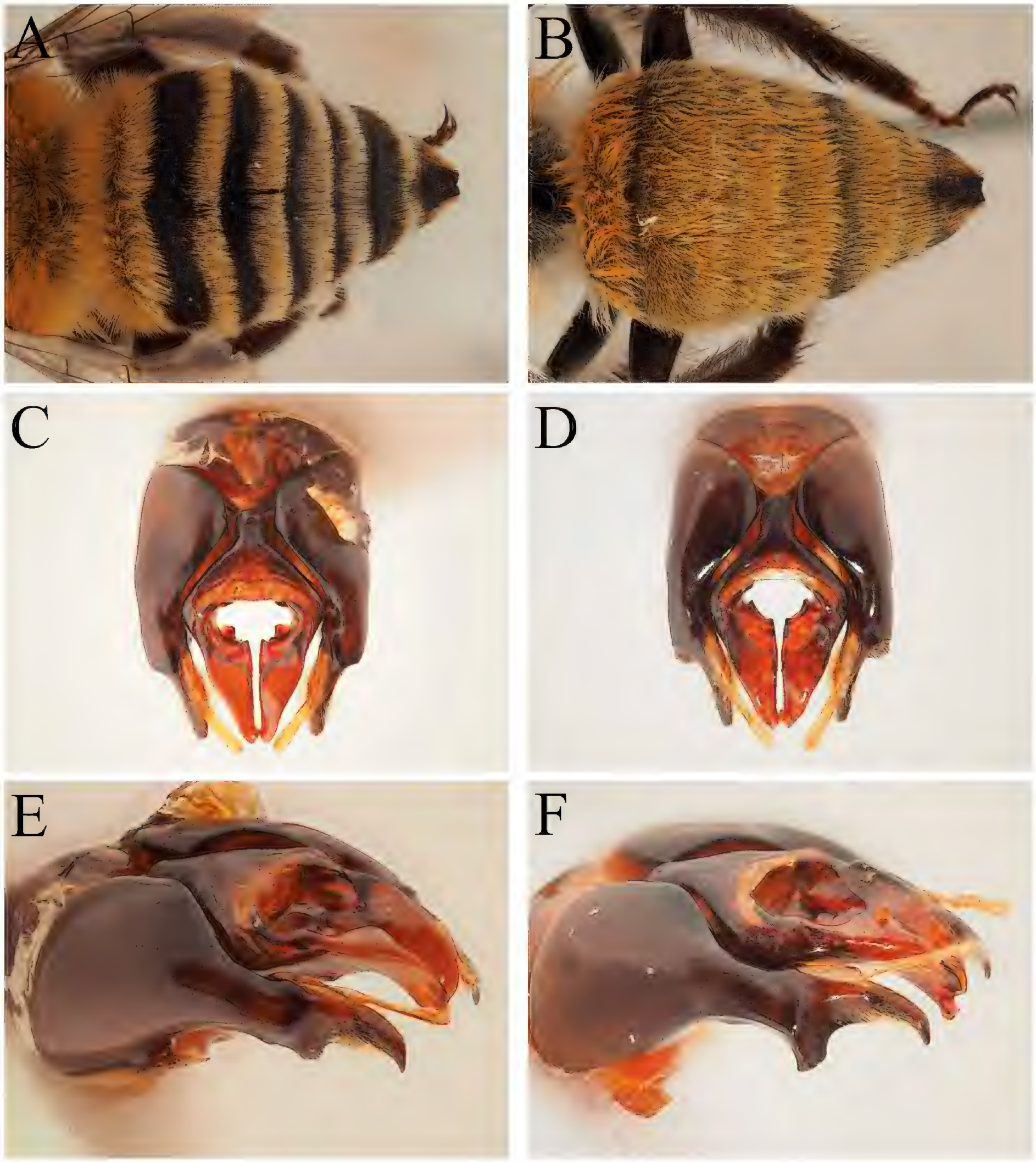

Figure 18. *Anthophora* (*Paramegilla*) *superans* Walker, 1871 male. **A.** Metasoma, dorsal view. **C.** Genital capsule, dorsal view. **E.** Genital capsule, dorso-lateral view. *Anthophora* (*Paramegilla*) *ferruginea* Lepeletier, 1841 male; **B.** Metasoma, dorsal view. **D.** Genital capsule, dorsal view. **F.** Genital capsule, dorso-lateral view.

Suppl. material 1). The two species can also be separated by their tergal pubescence (Fig. 18A, B).

For the specimens of *An. inclyta*, the situation is more complex. The three available female specimens are from the Convent Garden on Mount Sinai (Fig. 19A) and Rafla in Eritrea (Fig. 20A). Whilst morphologically similar, it is not clear if they are actually conspecific. One character often seen in the East Mediterranean taxon is that the female has a slightly raised longitudinal carina medially, which is sometimes coloured yellow, and the anterior margin of the clypeus slopes towards the apical margin with weak sculpturing, becoming almost shining. This is present in the specimens from Sinai but not in the specimen from Eritrea. Although the specimen from Eritrea was designated as the lectotype by Baker in 1979, this was never validly published, as with *An. superans*. Baker (1993: 310) selected the Eritrean specimen as the lectotype, as he considered the females from Sinai to be conspecific with *An. superans*.

Given the lack of a validly published lectotype, the existence of syntypic specimens from Sinai, and the fact

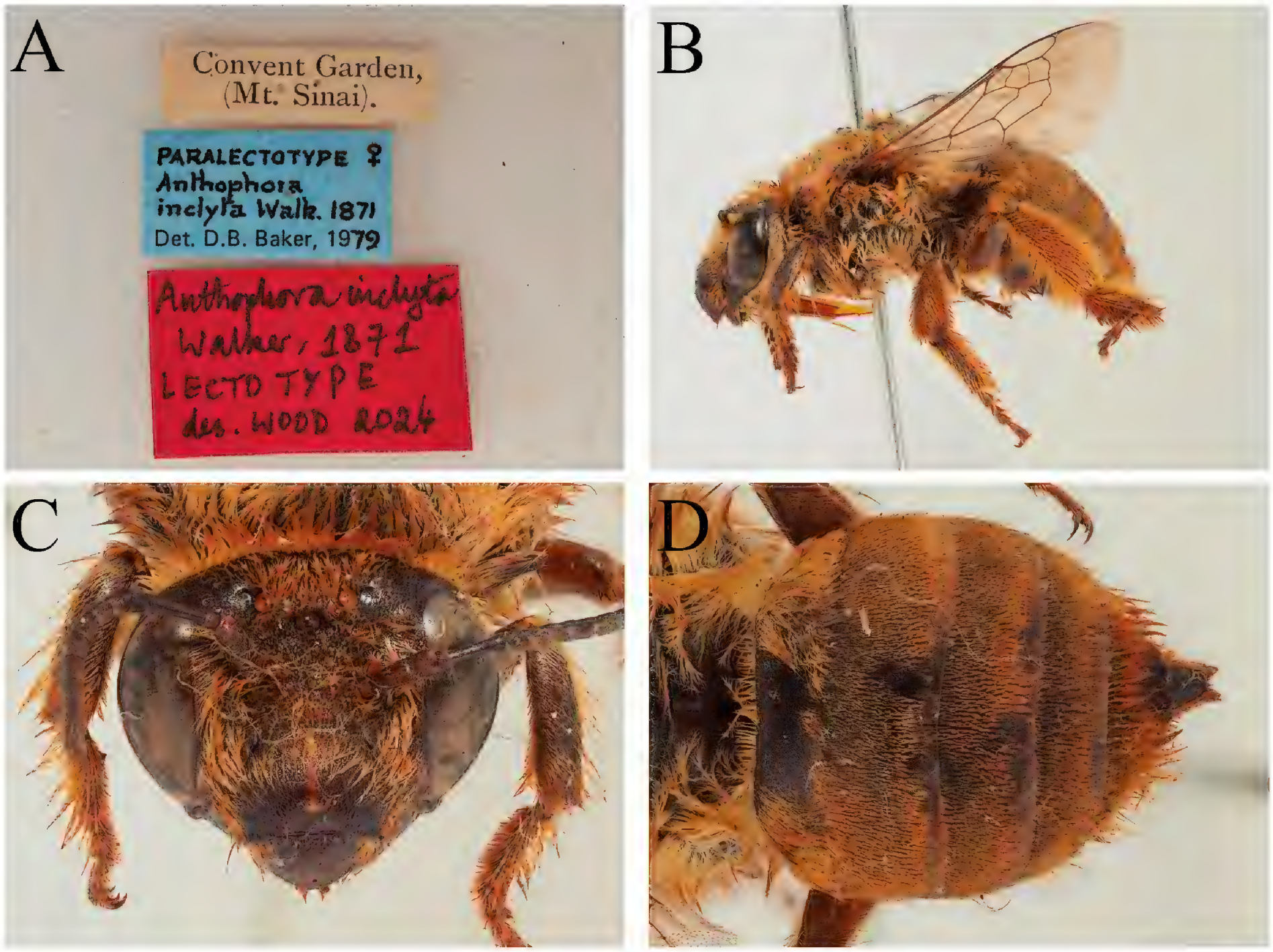

Figure 19. *Anthophora* (*Paramegilla*) *inclyta* Walker, 1871 female lectotype (NHMUK). **A.** Label details; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Metasoma, dorsal view.

that no one has previously acted as a first reviser in a way compliant with ICZN rules (Brooks 1988 considered both taxa as distinct), under Article 24.2, as First Reviser, we select a syntypic female of *An. inclyta* from the Convent Garden (Mount Sinai) as lectotype by present designation, and given the simultaneous publication of *An. superans* and *An. inclyta* by Walker (1871) with no objective way to determine precedence, we select *An. superans* to have precedence over *An. inclyta* syn. nov. Based on this synonymy and establishment of *An. superans* as the priority name for *An. dubia sensu auctorum* in the East Mediterranean, a total of 48♀ and 34♂ could be examined (including type material; see Suppl. material 1), producing a revised distribution of *An. superans* covering Italy (first record), Greece, Turkey, Armenia, Israel and the West Bank, and Egypt (Fig. 21), and (nominally based on its status as a syntype, though the specimen is probably not conspecific due to its differently sculptured clypeus; revision is required) Eritrea. The species is likely to be present in Jordan, Lebanon, Syria, and Iran once additional material has been studied. Baker (1993: 310) gave the range as "from the Balkans eastwards through the Levant to the Urals and Caucasus". We partially agree, citing a need to examine additional material from the Caucasus and Iran, though we consider the Ural Mountains implausible for ecological and biogeographical reasons given the apparent thermophilic tendencies of this East Mediterranean species.

Given the morphology of *An. superans*, it is relevant to consider the West Mediterranean *An. ferruginea*. This species is found in southern Spain, Morocco, Algeria, and Tunisia (Fig. 21; described from Oran in Algeria); it is particularly common in south-eastern Spain. Given the very scant label details of the MNCN paratype of *T. hellenicus*, it is not impossible that the specimen (the only known specimen of *T. hellenicus* collected in Spain) was actually from south-eastern Spain, rather than "Madrid". Indeed, we have never seen any *An. ferruginea* from the Madrid region, with other *Anthophora* (*Paramegilla*) species occurring there, such as *An. balneorum* and *An. femorata*. Given these uncertainties, we cautiously suggest *An. ferruginea* as a possible host of *T. hellenicus* in Spain, pending further study.

In conclusion, given the association between *T. hellenicus* and an *Anthophora* (*Paramegilla*) species, a subgenus strongly diversified in Turkey, Iran, the Caucasus, southern Russia, and Central Asia, it is difficult to comment on either (i) the overall eastern distribution of *T. hellenicus* or (ii) the number of closely related and insufficiently characterised *Thyreus* species that may be present in this area.

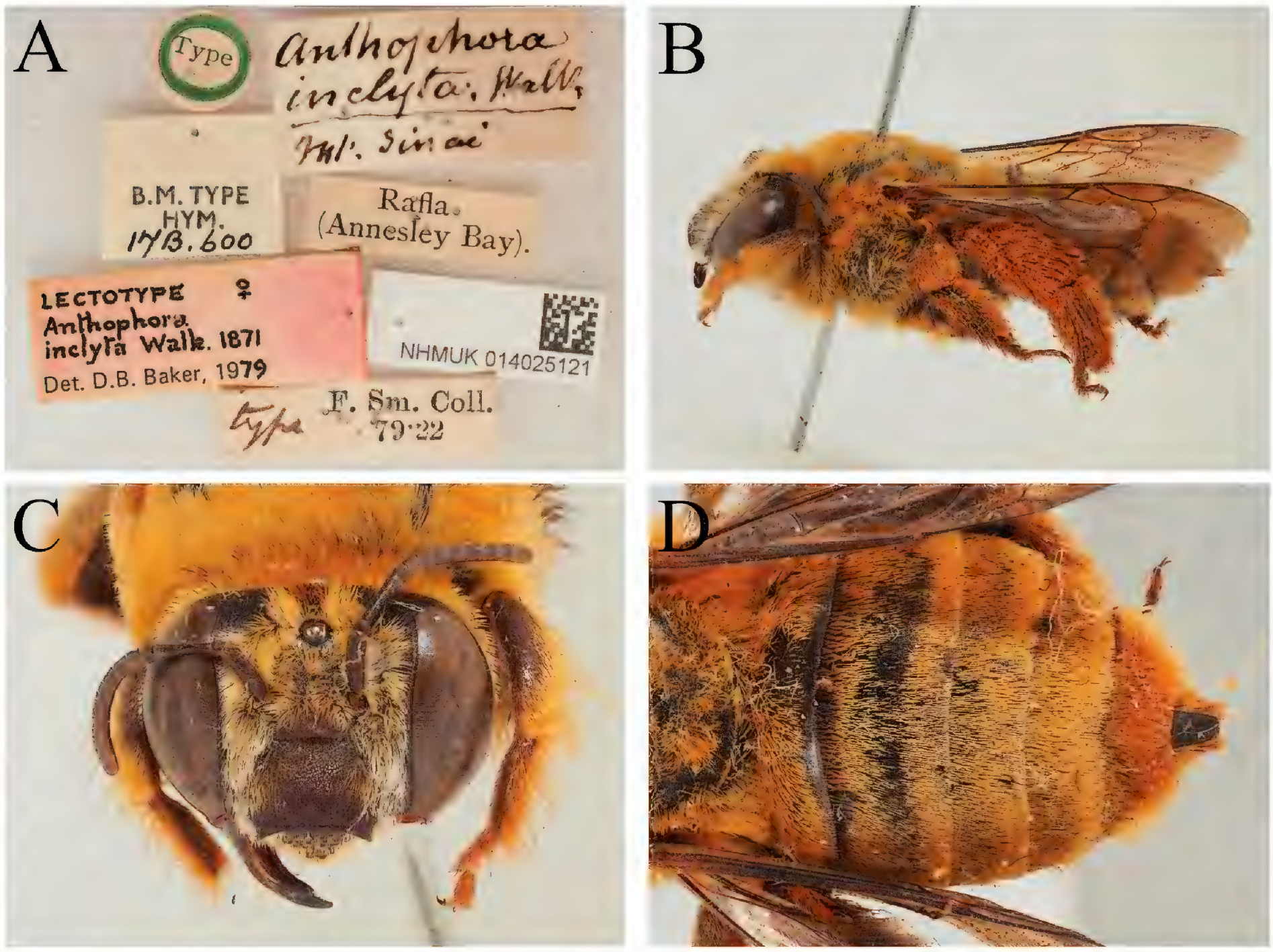

Figure 20. *Anthophora* (*Paramegilla*) *inclyta* Walker, 1871 female paralectotype (NHMUK). **A.** Label details; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Metasoma, dorsal view.

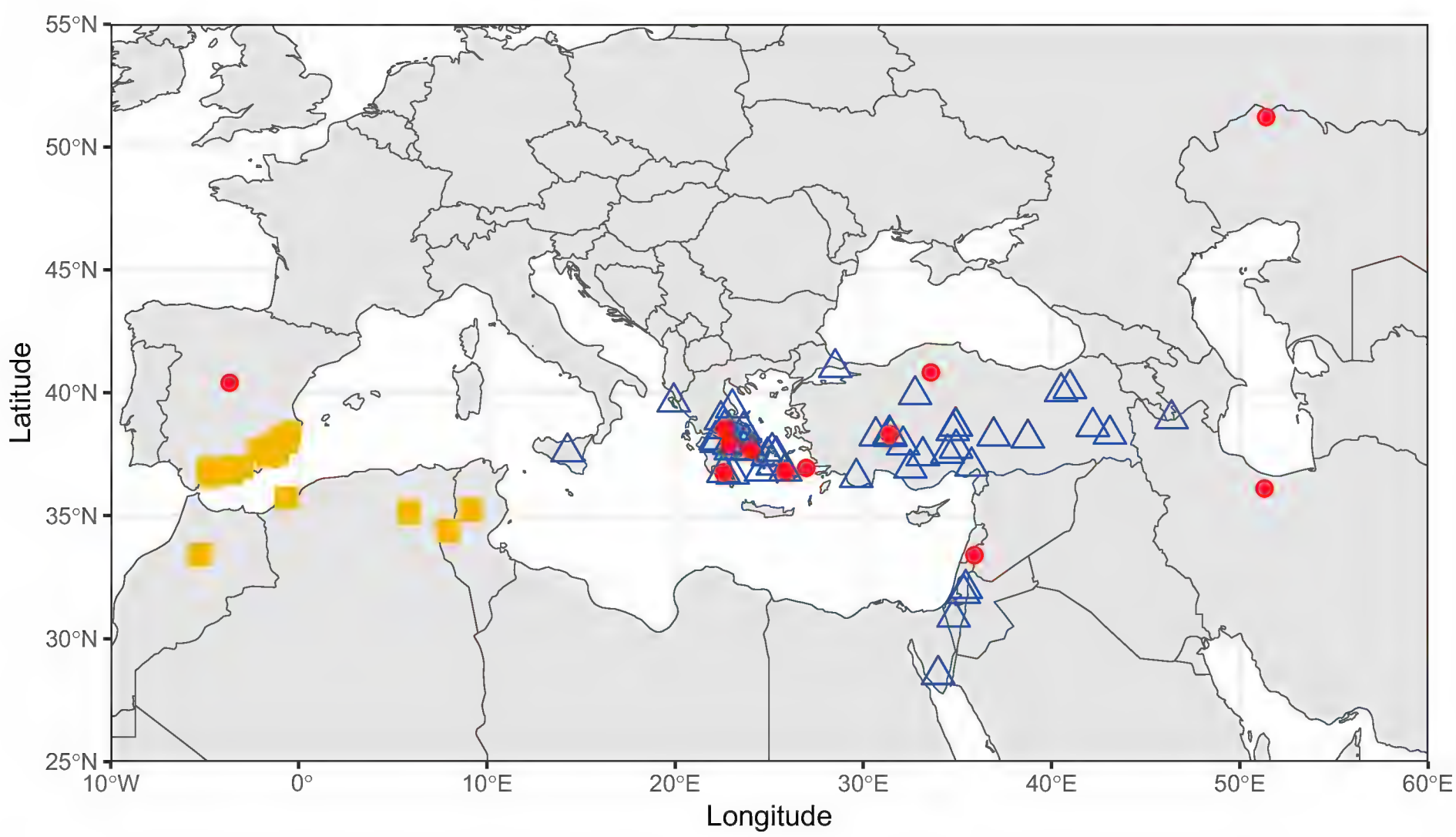

Figure 21. Distribution of *Thyreus hellenicus* Lieftinck, 1968 (red circles) along with its host *Anthophora* (*Paramegilla*) *superans* Walker, 1871 (open blue triangles) and possible host *Anthophora* (*Paramegilla*) *ferruginea* Lepeletier, 1841 (filled yellow squares). Distributional data are not comprehensive.

Distribution. Spain (precise location uncertain), Greece, Turkey, Syria, Iran, Kazakhstan (Lieftinck 1968; Ascher and Pickering 2025). The listing of Iran comes from material determined by Baker hosted in his collection at the Kansas museum. Given Baker's knowledge of this genus, we accept the record as plausible. Listings from Morocco, Liechtenstein, and Ukraine (Ascher and Pickering 2025) are from the American Museum of Natural History species database and are excluded at the present time due to a lack of precise supporting data.

Other material examined. *Anthophora superans* **Egypt** • 1♂; Convent Garden, Mount Sinai; NHMUK (***lectotype*** by present designation) • 2♂; Gebel Musa (Mt. Sinai) [Jabal Mousa]; NHMUK (***paralectotypes***) • 1♂; Sandy plains (Mt. Sinai); NHMUK (***paralectotype***); **Italy** • 1♀; Sicilia; 1858; Mann leg.; NHMW.

Anthophora inclyta **Egypt** • 2♀; Convent Garden, Mount Sinai; NHMUK (***lectotype*** by present designation and ***paralectotype***); **Eritrea** • 1♀; Rafla (Annesley Bay) [Arafali/Irafayle]; NHMUK (***paralectotype***).

Additional examined non-type specimens (all under the name *An. superans*) are presented in Suppl. material 1.

Thyreus hirtus (de Beaumont, 1940)

Crocisa hirta de Beaumont, 1940: 169, ♀♂ [Switzerland, NMB, not examined]

Material examined. Wood (2023) presented specimens of *Thyreus hirtus*; additional examined specimens are detailed in Suppl. material 1.

Notes. Lieftinck (1968) and Wood (2023) both gave the year of publication as 1939, but Berland (1940) clarified that only pages 1–108 (issues 1–2) were published on 20 Apr. 1939, with pages 109–184 (issues 3–4) published on 30 Apr. 1940. The year of publication is therefore 1940. Wood (2023) demonstrated that most records of *T. hirtus* from North Africa actually belong to *T. rasmonti* Wood, 2023, or were simply misidentified specimens of other species such as *Thyreus mauretaniensis* (Strand, 1911).

One unclear specimen mentioned by Lieftinck (1968: 90) was that of a male from Crete. This specimen is in the RMNH collection (RMNH.INS.1714260) and was re-examined and re-determined as *T. histrionicus*, as it has entirely white hair on the face and the genital capsule is typical for *T. histrionicus* (see key below for precise criteria). A further specimen from Sarepta (= Volgograd) in European Russia was also mentioned by Lieftinck as coming from the Amsterdam museum collection. Although this collection has been integrated into the RMNH collection, this particular specimen could not be located. Given the enormous distance between the nearest confirmed *T. hirtus* records in Italy and southern European Russia (some 2,500 km), this record is excluded on the grounds of improbability.

The revised distribution of *T. hirtus* is therefore clearly West Mediterranean (Fig. 22). This conforms to the distribution of two *Echium*-specialised *Anthophora* Latreille, 1803: *Anthophora* (*Paramegilla*) *balneorum* Lepeletier, 1841 and *Anthophora* (*Paramegilla*) *femorata* (Olivier, 1789) (Fig. 22), which are suspected to be the hosts (Baldock et al. 2018). Although we do not have conclusive evidence or direct observation of these taxa at nest sites, the circumstantial evidence is substantial: *T. hirtus* and *An. femorata* are particularly common together in north-western Iberia and south-eastern France, *T. hirtus* and *An. balneorum* in the western Alps, and the overall distributions map closely together. *Anthophora balneorum sensu lato* in North Africa requires taxonomic attention, which will be provided in short order (TJW, in prep).

Distribution. Portugal, Spain, France, Switzerland, Italy, Algeria (Lieftinck 1968 *partim*; Wood 2023; Fig. 22).

Thyreus praevalens (Kohl, 1905)

Crocisa praevalens Kohl, 1905: 243, ♂ [Turkey, NHMW, examined].

Material examined. **Armenia** • 1♀; Monastero Gherard [Geghard]; 13 Jul. 1963; A.G. Soika leg.; M.A. Lieftinck det. 1967; MNHN; **Greece** • 1♀; Stena Fourkas, 6 km S Lamia; 1000 m a.s.l.; 29 May 2005; M. Šárovec leg.; OÖLM; **Turkey** • 1♂; 2 km S Nevşehir; 1250 m a.s.l.; 4 Jul. 1984; A.W. Ebmer leg.; M.A. Lieftinck det.; RMNH; RMNH.INS.1714355 • 1♀; 5 km W Nevşehir; 1300 m a.s.l.; 19 Jul. 1984; A.W. Ebmer leg.; M.A. Lieftinck det.; RMNH; RMNH.INS.1714354 • 1♂; Erdschias (Illany-Dagh) [Yilanli Dağ, Kayseri]; Penther leg.; NHMW (***holotype***) • 1♂; Amasia [Amasya]; M.A. Lieftinck det. 1962; MNHN (ex. coll. Pérez 1915).

Notes. *Thyreus praevalens* is newly reported here for Greece and thus for Europe. Lieftinck (1968: 71) confusingly wrote about the pubescence of the clypeus in a non-type specimen "… it has the clypeal pubescence [sic] black; not white as might appear from the original diagnosis". This factors into the key, where he indicates that the species is partially separated from *T. hellenicus* due to the dark facial hair (Lieftinck 1968: 16, couplet 4; 17, footnote), and indeed, inspected female specimens of *T. praevalens* do present such hairs (Fig. 23B). However, the male holotype of *T. praevalens* has not a single black hair on the face (Fig. 24C, D). The colouration of the facial hair does seem variable, as males with light and dark facial hair appear to be structurally identical. Lieftinck (1968: 70) points out as a key character the punctation of the vertex behind the ocellar triangle, which is extremely dense and contrasts with the almost impunctate areas adjacent to the lateral ocelli in both sexes (Fig. 23E, F). This pattern of punctation is similar to that observed in *T. hellenicus*. In short, the characters most important for diagnosis seem to be the punctation of the vertex combined with the shape of the scutellum (Fig. 23C) and the shape of the white markings on T1 (Fig. 23D). This information is integrated into the identification key below.

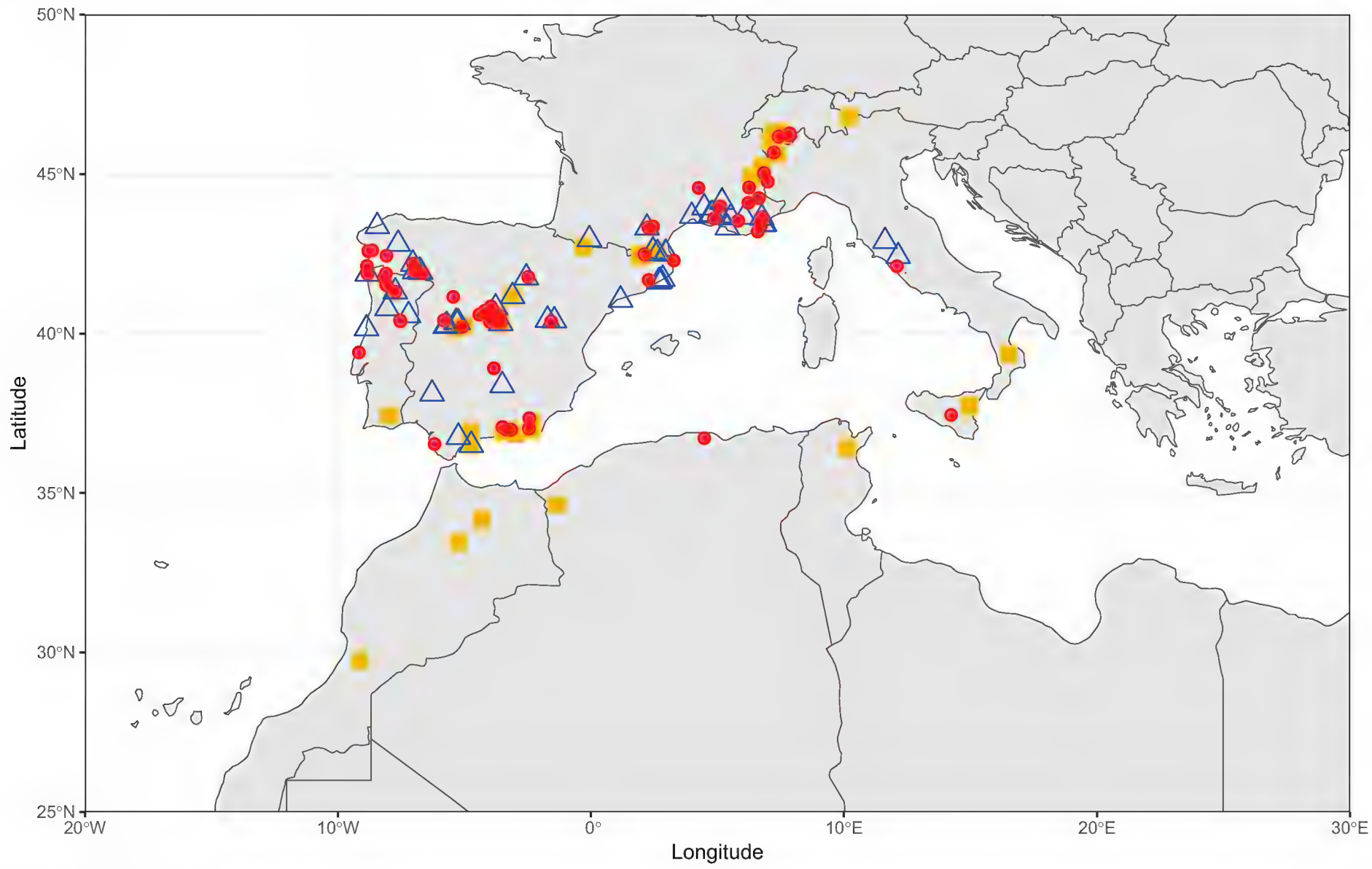

Figure 22. Distribution of *Thyreus hirtus* (Beaumont, 1940) (red circles) along with its two hosts, *Anthophora femorata* (Olivier, 1789) (open blue triangles) and *Anthophora balneorum* Lepeletier, 1841 (filled yellow squares). Distributional data are not comprehensive.

Given the observed distribution, the close morphological similarity to *T. hellenicus*, which attacks *Anthophora* (*Paramegilla*) species, the small number of *Paramegilla* species present in Greece, and the flight period, there is circumstantial evidence to suggest that the host of *T. praevalens* may be *Anthophora* (*Paramegilla*) *onosmarum* Morawitz, 1875, which was recently reported as new for Turkey, southern Bulgaria, and northern Greece (Wood and Praz 2024). Further study is required.

Distribution. Greece*, Turkey, Armenia (Lieftinck 1968).

Thyreus hohmanni Schwarz, 1993

Thyreus hohmanni Schwarz, 1993: 869, ♀♂ [Spain: Gran Canaria, LRC, not examined].

Material examined. Spain • 2♀; Gran Canaria, Ayacata; 14 Jun. 1995; M. Hradský leg.; B. Tkalců det.; OÖLM • 1♀; Gran Canaria, Fataga; 5 Sep. 1993; F. La Roche leg.; F. La Roche det.; OÖLM • 1♂; Gran Canaria, Moya; 8 Apr. 1985; J. Correa leg.; B. Tkalců det.; OÖLM • 1♀; Gran Canaria, Presa de los Hornos; 16 Jun. 1995; M. Hradský leg.; OÖLM • 1♀; Gran Canaria, Teror; 8 Dec. 1986; F. La Roche leg.; F. La Roche det.; OÖLM • 1♂; Canarias [no further information]; MNCN • 1♂; Gran Canaria, El Sao; 17 Sep. 1941; MNCN.

Notes. *Thyreus hohmanni* is unusual in that it shows a distribution seemingly restricted entirely to the island of Gran Canaria. The logical host would seem to be *Amegilla* (*Amegilla*) *canifrons* (Smith, 1854), but this species can be found on the islands of both Gran Canaria and Tenerife, with an uncertain record from La Palma (Dusmet 1924; Lieftinck 1958). To date, no specimens of *T. hohmanni* have been found on Tenerife; it may never have reached this island or may have disappeared at some point after its emergence as a distinct species. New records not included in Schwarz (1993) are presented here, supporting its position as an endemic of this single island.

Distribution. Spain (Gran Canaria) (Schwarz 1993).

Thyreus scutellaris (Fabricius, 1781)

Nomada scutellaris Fabricius, 1781: 487, ♂ [Siberia, NHMD, not examined].

Material examined. Kazakhstan • 3♂, 4♀; NO, Bajanaul NP; 410 m a.s.l.; 22 Jun. 2008; W-H. Liebig leg.; TJWC/WHLC • 6♂; NO, Bajanaul NP; 410 m a.s.l.; 24 Jun. 2024; W-H. Liebig leg.; TJWC/WHLC • 5♂, 1♀; NO, Bajanaul NP; 410 m a.s.l.; 20 Jun. 2008; W-H. Liebig leg.; WHLC • 4♂, 1♀; NO, Bajanaul NP; 410–443 a.s.l. m; 15–21 Jun. 2008; W-H. Liebig leg.; WHLC • 2♂, 1♀; NO, Bajanaul NP; 410–443 a.s.l. m; 23 Jun. 2008; W-H. Liebig leg.; WHLC • 1♂; SE, Kokterek, 18 km NW; 475 m a.s.l.; 11 Jun. 2024; W-H. Liebig leg.; WHLC • 2♂, 1♀; SE, Kokterek, 20 km E; 475 m a.s.l.; 10 Jun. 2024; C. Schmid-Egger & W-H. Liebig leg.; CSE/WHLC • 1♂; SE, Shonzhy 10 km NW;

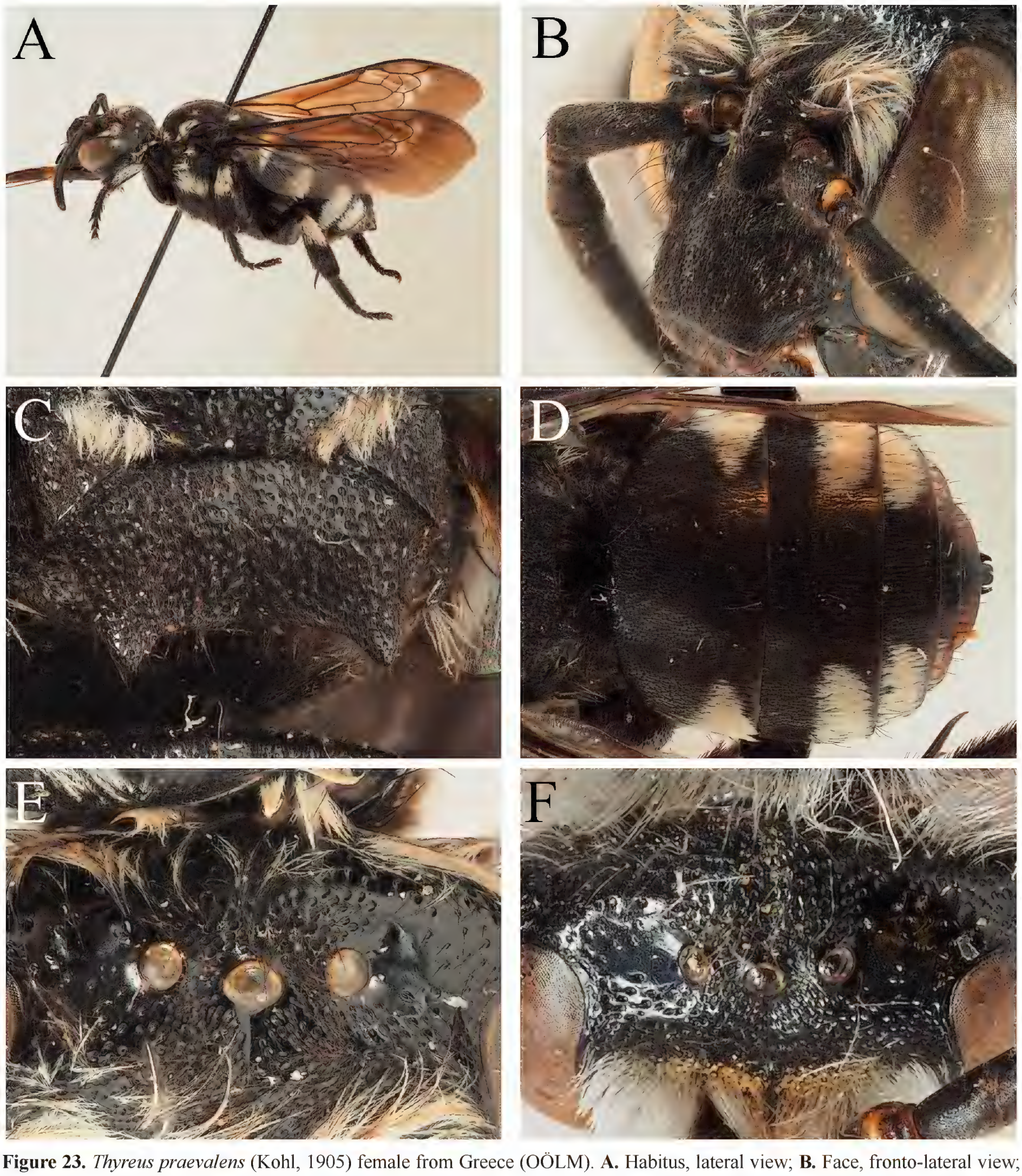

Figure 23. *Thyreus praevalens* (Kohl, 1905) female from Greece (OÖLM). **A.** Habitus, lateral view; **B.** Face, fronto-lateral view; **C.** Scutellum, dorsal view; **D.** Terga, dorsal view; **E.** Vertex and ocellar triangle, dorsal view. *Thyreus praevalens* (Kohl, 1905) male holotype (NHMW); **F.** Vertex and ocellar triangle, dorsal view.

654 m a.s.l.; 3 Jun. 2024; W-H. Liebig leg.; WHLC • 1♂; SE, 12 km SE Zhalgyzagash; 1322 m a.s.l.; 8 Jun. 2024; C. Schmid-Egger leg.; CSE; **Russia** • 1♂; Baikalgebeit, Ust-Orda [Ust'-Ordynskii] ostl.; 545 m a.s.l.; 26 Jun. 2011; W-H. Liebig leg.; WHLC • 1♀; БАССР [Baskhir], Уфа [Ufa]; 18 Jul. 1959; D.B. Baker det. 1959; RMNH; RMNH.INS.1662717; BOLD accession number BGENL2290-24.

Notes. The concept of *T. scutellaris* has changed over time. Prior to the work of de Beaumont (1940) and Alfken (1940), the name *T. scutellaris* was applied to what is today called *T. orbatus* (Lepeletier, 1841) (Lieftinck 1959b; 1968). The range has therefore been confused in the literature. Records from Portugal (Dusmet 1931; Diniz 1959) and Romania (Iuga 1958) clearly refer to this pre-de Beaumont concept of *T. scutellaris*. Iuga (1958: 220) even referred to *Anthophora vulpina* (Panzer, 1798) (recte *Anthophora quadrimaculata* (Panzer, 1798)) as the host of "*T. scutellaris*", another indication that they were referring to *T. orbatus*, which is well known to attack this species of *Anthophora* (e.g. Lieftinck 1968; Amiet et al. 2007).

Figure 24. *Thyreus praevalens* (Kohl, 1905) male holotype (NHMW). **A.** Label details; **B.** Habitus, lateral view; **C.** Head, frontal view; **D.** Head, lateral view; **E.** Scutum, dorsolateral view; **F.** Metasoma, dorsal view.

Based on the newly examined specimens, we hypothesise a possible host through examination of concurrently active and captured Anthophorinae. At Bajanaul (2008) and at Lake Baikal (2011), *T. scutellaris* was captured with *Anthophora* (*Mystacanthophora*) *meridionalis* Fedchenko, 1875, by W-H. Liebig (specimens WHLC). Active at most capture sites in Kazakhstan (2024) were numerous species of *Anthophora* (*Paramegilla*) Friese, 1897, though these seem less likely to be hosts due to (i) their large size relative to *T. scutellaris* and (ii) their thermophilic tendencies, with most *Paramegilla* species favouring warm to hot grasslands and not extending into cooler parts of Siberia where *T. scutellaris* is also present. Clearly, additional focused study is required, but this circumstantial evidence forms the basis for a testable hypothesis.

Lieftinck (1968) redefined the global range as predominantly Asian. In Europe, outside of European Russia, there is a single record from Croatia from 1886 (Lieftinck 1968); to our knowledge, the next nearest records come from Turkey and Russia (Astrakhan). Lieftinck's records from Egypt, "Syria", and Arabia are difficult to understand for biogeographical reasons. Most records of *T. scutellaris*, including the original *terra typica*, come

from areas with a strongly continental climate, including cold winters. Molecular characterisation, along with additional study of Near Eastern specimens, is necessary to more fully understand the southern range limit of this species as well as its potential host(s).

Distribution. ?Egypt, ?Syria sensu lato, ?Arabia sensu lato, Croatia, Russia (European part, Urals, Western Siberia, Eastern Siberia), Turkey, Iran, Turkmenistan, Kazakhstan, Afghanistan, Mongolia, China (Gansu, Inner Mongolia) (Lieftinck 1959b, 1968).

Identification key for European *Thyreus* species

The key of Lieftinck (1968) contains good information in large part but is challenging to use due to the broad geographic scope (from North Africa to China and the Korean Peninsula), the use of too many characters of variable importance, and most of all, the inclusion of males and females in the same key. This limits the ability of the user to swiftly recognise species groups, such as the *scutellaris*-group, based on the male genitalia, resulting in related species being scattered across widely separated parts of the key.

The following key aims to extract the most salient information from Lieftinck (1968) within a narrower geographic scope, specifically that of Europe. Distributional information in the key refers only to the European range, and the broader work of Lieftinck (1968) should be consulted for non-European distributions. For males, it is strongly advised to extract the genital capsule (all species) and to examine the lobes of the 8th sterna (certain species). Despite the use of genitalia characters by de Beaumont (1940), some previous keys (e.g. Vergés 1967; Amiet et al. 2007) have not referred to the male genital capsule at all, which presents difficulties for *Thyreus* given the high level of difficulty rendered by a reliance on external morphology. Additional non-genital characters are given in the male key, but their use in isolation may lead to incorrect identifications.

In addition to the images presented here, good illustrations and additional characters and perspectives can be found in de Beaumont (1940), Lieftinck (1968), Schwarz (1993), and Amiet et al. (2007). Female specimens are inherently more difficult to identify, and abraded specimens are often impossible; confidently determined or barcoded reference specimens should be consulted whenever possible.

1 Six visible terga, 12 antennomeres; females 2
– Seven visible terga, 13 antennomeres; males 13
2 (1) Body predominantly covered in dense adpressed white pubescence that obscures the underlying surface, in dorsal view approximately 75% of tergal surfaces covered in such pubescence (Fig. 25A). Scutellum posteriorly produced into two very long acute points, these forming a deep U-shaped emargination (Fig. 25B). Outer margins of axillae slightly detached from outer margin of scutellum, forming moderately acute points. Found only on Cyprus ..... *T. elegans* (Morawitz)
– Body with white pubescence, but never covering a majority of the surface, terga always predominantly dark. Scutellum posteriorly produced into blunt or rounded points, or if produced into acute points then with the median emargination much shallower (Fig. 25D). Outer margins of axillae either flush with outer margin of scutellum (e.g. Fig. 25F) or forming small sharp points (e.g. Fig. 25D). Found on Cyprus or not 3
3 (2) T1 with four distinct and elongate white hair patches, two placed basally and two apically, forming widely interrupted basal and apical hairbands; bands clearly separated (interrupted) by black hairs on lateral margins (Fig. 25C, E) 4
– T1 with two distinct white hair patches placed laterally (Fig. 27A, B), these either C-shaped or L-shaped, widely interrupted medially in the centre of the disc; always with continuous white hairs on the lateral parts of the disc (uninterrupted) 5
4 (3) Posterior margin of scutellum distinctly impressed medially, disc of scutellum thus not flattened, distinctly biconvex (Fig. 25D). Scutellum posteriorly produced into sharp acute points. Outer margins of axillae slightly detached from outer margin of scutellum, forming small sharp points. Rare in Europe, known as far west as Croatia, probably persisting mostly in European Russia ..... *T. scutellaris* (Fabricius)
– Scutellum evenly flattened, posterior margin of scutellum not depressed medially (Fig. 25F). Scutellum posteriorly produced into blunt 90° points. Outer margin of axillae flush with outer margin of scutellum, not produced into a point. Widespread across southern Europe from Portugal to Bulgaria, Greece, and Cyprus, north to the Pannonian basin ..... *T. affinis* (Morawitz)
5 (3) Scutum laterally with a continuous band of short white hairs running up to the junction with the axillae (Fig. 26A) Small, always < 10 mm in length ..... *T. ramosus* (Lepeletier)
– Scutum laterally never with an unbroken band of white hairs, always with some black hairs (Fig. 26B). Larger, usually > 10 mm in length, though some small specimens of *T. truncatus* can be 9 mm in length 6
6 (5) Found on the island of Gran Canaria (Canary Islands) ..... 7[1]
– Found elsewhere in Europe, including other Canarian islands 8

1 Due to the restricted geographic distribution, *T. hohmanni* is keyed out here; most workers will never encounter this species.

7 (6) Face with abundant short black pubescence below the antennal insertions. T1, when viewed dorsally with narrow L-shaped white hair patches laterally, these barely extending towards the centre of the disc at its base. Scutellum densely punctate, punctures separated by ≤ 0.5 puncture diameters ..... *T. hohmanni* Schwarz

– Face entirely white-haired. T1, when viewed dorsally with broad C-shaped white hair patches laterally, these extending inwards towards the centre of the disc almost as much at the base of the disc as on the marginal area (Fig. 27A). Scutellum more sparsely punctate with punctures separated by 0.5–1 puncture diameters, interspaces polished and shining ..... *T. histrionicus* (Illiger) (*partim*)

8 (6) Found in Greece with the following combination of characters: scutellum short and broad, medially with a narrow but deep sulcate impression, surface densely punctate, punctures separated by ≤ 0.5 puncture diameters (Fig. 23C). Vertex behind ocellar triangle densely punctate, punctures separated by 0.5 puncture diameters, strongly contrasting areas adjacent to lateral ocelli, which are polished, shining, and almost impunctate (Fig. 23E). T1 viewed dorsally with small triangular hair patches, these barely extending towards the base of the tergum (Fig. 23D). Antenna with rhinaria elongate lanceolate, longitudinally-orientated, and placed on the ventral surface of the antenna. Face below antennal insertions with abundant dark pubescence (Fig. 23B) ..... *T. praevalens* (Kohl)[2]

– Distribution or combination of characters not as above ..... 9[3]

9 (8) Face below antennal insertions usually with abundant black hairs (Fig. 26C), but some specimens of *T. orbatus* from southern Spain (Sierra Nevada) present faces with abundant white pubescence and only a few scattered black hairs. For *T. orbatus*, if in doubt, then lateral white hair patch of T3 interrupted (Fig. 26D), distinctly interrupted by black hairs and thus forming two distinctly separated white hair patches 10

– Face below antennal insertions always white-haired (Fig. 26E), either entirely white-haired or at most with only a few scattered black hairs. Lateral white hair patch of T3 always entire, never broken into two distinct white hair patches 11

10 (9) Lateral white hair patch of T3 interrupted, distinctly interrupted by black hairs and thus forming two distinct white hair patches (Fig. 26D). Usually a little smaller, range 8–10 mm. Associated with *Anthophora quadrimaculata*. The most northerly *Thyreus* species, extending from the mountains of southern Europe into the Low Countries and northern Germany, as well as east to the Balkan Peninsula ..... *T. orbatus* (Lepeletier)

– Lateral white hair patch of T3 always entire, never broken into two distinct white hair patches (Fig. 26F). Usually a little larger, range 10–12 mm. Associated with *Echium*-specialised *Anthophora* (*Paramegilla*) species. Restricted to the West Mediterranean north to southern Switzerland ..... *T. hirtus* (de Beaumont)

11 (9) T1, when viewed dorsally with broad C-shaped white hair patches laterally, these extending inwards towards the centre of the disc almost as much at the base of the disc as on the marginal area (Fig. 27A). Scutellum moderately densely punctate, punctures separated by 0.5–1 puncture diameters, interspaces polished and shining (Fig. 27C) ..... *T. histrionicus* (Illiger) (*partim*) and *picaron* Lieftinck (females currently inseparable)

– T1 when viewed dorsally with narrow L-shaped white hair patches laterally, these extending inwards towards the centre of the disc only on the marginal area (Figs 7F, 9F, 27B). Scutellum very densely punctate, punctures separated by ≤ 0.5 puncture diameters, interspaces weakly shining to dull (Figs 7E, 9E, 27D) 12

12 (11) Smaller species, body length range 9–12 mm. Rhinaria absent. Scutellum short and broad, surface almost flat, posterior angles blunt and poorly indicated (Figs 7E, 9E). Associated with *Tetralonia dentata.* Widespread across continental Europe ..... *T. truncatus* (Pérez)

– Larger species, body length around 15 mm. Without rhinaria, but with a series of low longitudinal ridges. Scutellum longer, posterior angles more strongly produced (Fig. 27D). Associated with *Anthophora superans*. Predominantly in Greece, including the islands, but possibly also southern Spain ..... *T. hellenicus* Lieftinck

13 (1) Genital capsule simple, with gonostylus broadly triangular or produced into an acute point; never with an additional dorsal projection (Figs 2F, 28A, B). Gonostylus almost hairless, never with long hairs. T1 with hairs present basally and apically, forming either a complete basal and nearly complete apical bands (Fig. 29A) or with bands interrupted medially and separated laterally, thus appearing to form four distinct hair patches (Fig. 29B) (*scutellaris*-group) ...14

– Genital capsule complex, with gonostylus presenting a rounded or truncate apex (Figs 3H, 28C–H); gonostylus often with an additional basodorsal projection roughly at a 90° angle to the largest lobe of the gonostylus (Figs 3H, 28C–E). Gonostylus with long hairs, these often abundant and covering and obscuring the surface (Figs 3H, 28C–H). T1 with hairs variable, but never forming a complete basal band and always complete laterally, thus never forming four distinct hair patches 16

2 *Thyreus praevalens* is keyed out here through a combination of characters; whilst it could potentially be included in the following couplet based on the dark facial pubescence, it remains unclear if this is a robust character, and so a cautious approach is taken here.

3 Separation of the following six species depends heavily on pubescence characters, which are necessarily dependent on specimen condition. No attempt should be made to try and identify strongly abraded specimens, and association with concurrently active males should be made where possible.

14 (13) Body abundantly white-haired, particularly thickly covering the face (including frons), mesepisternum, and anterior ½ of scutum, obscuring the underlying surface. T1 with hairs forming a complete basal band and almost complete apical band, these bands connected laterally (Fig. 29A). T2 with broad apical hairband covering ½ the length of the tergum, only narrowly interrupted medially. Found only on Cyprus ..... *T. elegans* (Morawitz)

– Body without abundant white pubescence, only moderately hairy, white hairs of face, mesepisternum, and scutum not obscuring underlying integument. T1 with four distinct and elongate white hair patches, two placed basally and two apically, forming widely interrupted basal and apical hairbands (Fig. 29B). Found on Cyprus or not 15

15 (14) Posterior margin of scutellum distinctly impressed medially, disc of scutellum thus not flat, distinctly biconvex (as in Fig. 4C). Scutellum posteriorly produced into sharp acute points, medially with loose thin whitish hairs on dorsal surface, these not obscuring the underlying surface. Outer margin of axillae slightly detached from outer margin of scutellum, produced into a subtle but distinct point (as in Fig. 4C). Rare in Europe, known as far west as Croatia, probably persisting mostly in European Russia ..... *T. scutellaris* (Fabricius)

– Scutellum evenly flat, posterior margin of scutellum not depressed medially. Scutellum posteriorly produced into blunt ~90° points, medially with distinct patch of adpressed thick white hairs which obscures the underlying surface (Fig. 29C; may be abraded in old specimens). Outer margin of axillae flush with outer margin of scutellum, not produced into a point. Widespread across southern Europe from Portugal to Bulgaria, Greece, and Cyprus, north to the Pannonian basin ..... *T. affinis* (Morawitz)

16 (13) In lateral view, gonostylus distinctly bifurcate, with a large apically projecting and truncate lobe and basal detached and dorsally projecting acutely pointed lobe oriented roughly 90° relative to the truncate lobe (Fig. 3H, 28C–E) 17

– In lateral view, gonostylus with only a single apically projecting lobe, never with a distinct detached dorsally projecting lobe (Fig. 28F–H)..... 20

17 (16) Apical projections of S8 slender with distinct 90° bend, thus appearing distinctly "L-shaped" (Fig. 3F)..... ..... *T. picaron* Lieftinck

– Apical projections of S8 parallel-sided, apexes truncate to rounded (Fig. 29D) 18

18 (17) Face with abundant black hairs on the face below the antennal insertions. In dorsal view, lateral margins of T1 with white hairs loose, not adpressed, laterally erect and projecting thus contrasting the white hairs on the marginal area of T1 which are adpressed, obscuring the underlying surface (Fig. 29E). Restricted to the West Mediterranean north to southern Switzerland ..... *T. hirtus* (de Beaumont)

– Face entirely white-haired. In dorsal view, lateral margins of T1 with white hairs adpressed, not differentiated from adpressed white hairs on the marginal area of T1 (Fig. 29F). Widespread throughout Europe 19

19 (18) Genital capsule with dorsal projection strongly produced, standing distinctly away from outer margin of gonocoxa, with long hairs, length of these hairs at least twice the breadth of the dorsal projection (Fig. 28D). Main lobe of gonostylus with abundant long hairs; in lateral view, hairs projecting beyond the apex of the gonostylus by a distance equal to the maximum breadth of the hind basitarsus (Fig. 30A) ..... *T. histrionicus* (Illiger)

– Genital capsule with dorsal projection weakly produced, not strongly isolated from outer margin of gonocoxa, with short hairs, these hairs equalling or only slightly exceeding breath of the dorsal projection (Fig. 28E). Main lobe of gonostylus with abundant but short hairs; in lateral view, hairs only slightly projecting by much less than the maximum breadth of the hind basitarsus (Fig. 30B) ..... *T. truncatus* (Pérez)

20 (16) Scutellum short and broad, medially distinctly impressed and narrowly sulcate (Fig. 24E). T1 viewed dorsally with small apicolateral triangular hair patches, not extending towards base of tergum (Fig. 24F). Vertex behind ocellar triangle densely punctate, punctures separated by 0.5 puncture diameters, strongly contrasting areas adjacent to lateral ocelli, which are polished, shining, and almost impunctate (Fig. 23F). Found only in Greece.. ..... *T. praevalens* (Kohl)

– Scutellum flat, without such a median sulcate impression. T1 viewed dorsally with hair patches narrow or broad, but always extending to the base of the tergum. Vertex without such strongly contrasting punctation. Distribution variable 21

21 (20) Face below the antennal insertions usually with abundant black hairs (cf. Fig. 26C). In well-preserved specimens, T3 laterally with white band interrupted, thus forming two distinct white hair patches (Fig. 30C). Hind tibia ventrally produced into a small but distinct sharply pointed tooth overlying outer tibial spur (difficult to see without practice). Genitalia as in Fig. 28F. The most northerly *Thyreus* species, extending from the mountains of southern Europe into the Low Countries and northern Germany to around 52°N ..... *T. orbatus* (Lepeletier)

– Face below the antennal insertions never with abundant black hairs (Figs 15C, 16B). T3 laterally with a single unbroken white hairband (Figs 15B, 16B, 30D). Hind tibia without such a ventrally projecting tooth. Genitalia as in Figs 15E and 30E–F. Not extending north of 49°N 22

22 (21) Genital capsule with gonostylus long, in lateral view gonostylus elongate triangular, strongly projecting away from the gonocoxa by a distance exceeding the maximum breadth of a hind basitarsus (Fig. 15F). In dorsal view, the

long gonostyli give the genital capsule a rhomboidal appearance (Fig. 15E). Large, body length around 15 mm. Restricted to Greece, including the islands..... *T. hellenicus* Lieftinck

– Genital capsule more compact, gonostylus short, in lateral view gonostylus barely projecting beyond the gonocoxae. In dorsal view, genital capsule ovoid or rounded (Fig. 28G, H). Either large bodied (12–13 mm), in which case found only on the Canary Islands, or if found in continental Europe, then smaller, < 10 mm in length..... 23

23 (22) T7 with apical margin emarginate, emargination rounded rectangular, broader than deep (Fig. 30E). Smaller, body length < 10 mm. Widespread across continental Europe, but not present on the Canary Islands..... *T. ramosus* (Lepeletier)

– T7 with apical margin emarginate, emargination evenly rounded (Fig. 30F). Large, body length 12–13 mm. Restricted to Gran Canaria (Canary Islands) ..... *T. hohmanni* Schwarz

Figure 25. *Thyreus elegans* (Morawitz, 1877) female. **A.** Metasoma, dorsal view; **B.** Scutellum, dorsal view. *Thyreus scutellaris* (Fabricius, 1781) female; **C.** T1, dorsal view; **D.** Scutellum, dorsal view. *Thyreus affinis* (Morawitz, 1873) female; **E.** T1, dorsal view; **F.** Scutellum, dorsal view.

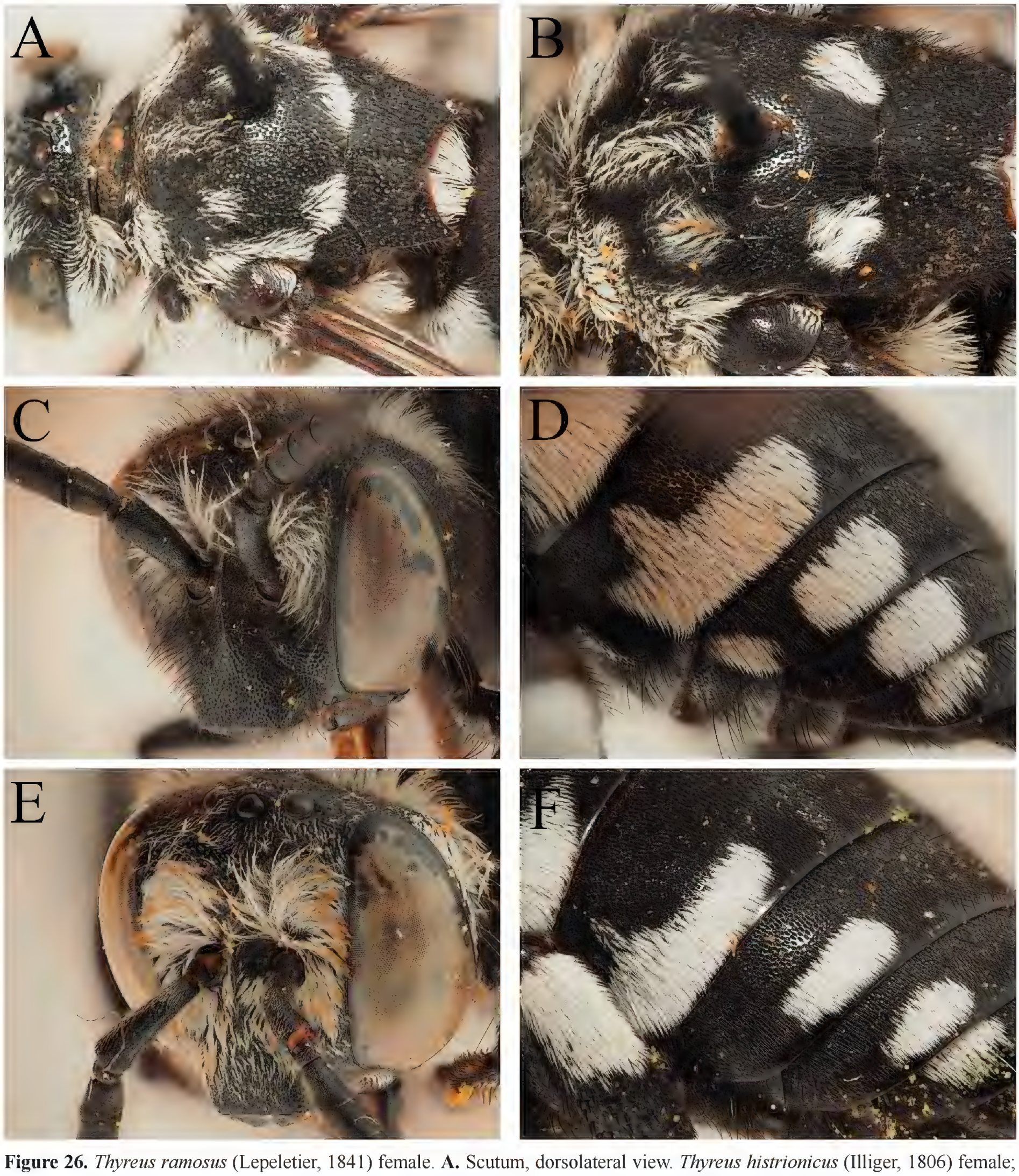

Figure 26. *Thyreus ramosus* (Lepeletier, 1841) female. **A.** Scutum, dorsolateral view. *Thyreus histrionicus* (Illiger, 1806) female; **B.** Scutum, dorsolateral view; **E.** Head, fronto-lateral view. *Thyreus hirtus* (Beaumont, 1940) female; **C.** Head, fronto-lateral view, **F.** Metasoma, lateral view. *Thyreus orbatus* (Lepeletier, 1841) female; **D.** Metasoma, lateral view.

Discussion

The results presented here and the taxonomic concepts refined through the inclusion of COI DNA barcoding overall support the taxonomic framework of Lieftinck (1968) for the West and Central Palaearctic species studied to date. The small number of changes necessary have related to minor errors in distributions resulting from misidentified or cryptic species, and the inclusion of genetic data and concurrent study with their predominantly anthophorine hosts has allowed range limits to be characterised with greater confidence.

Although most tropical species of *Thyreus* are likely to exclusively attack *Amegilla* due to the absence of

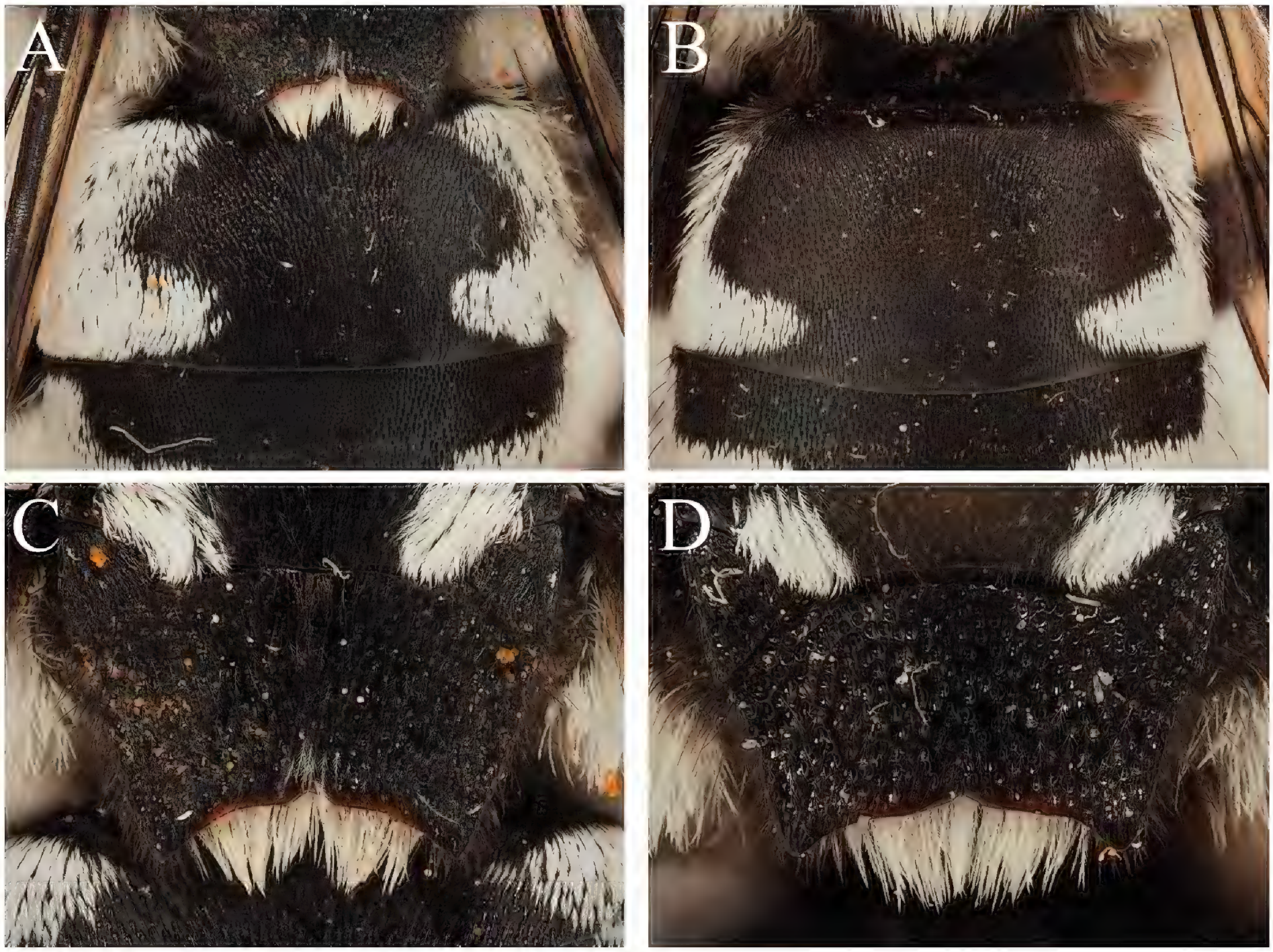

Figure 27. *Thyreus histrionicus* (Illiger, 1806) female; **A.** T1, dorsal view; **C.** Scutellum, dorsal view. *Thyreus hellenicus* Lieftinck, 1968, female; **B.** T1, dorsal view; **D.** Scutellum, dorsal view.

the genus *Anthophora* in very humid areas (for example, in most of South East Asia and all of Australasia; Brooks 1988), the pattern in the Palaearctic is much more mixed. Species known or suspected to attack *Anthophora* include *T. hellenicus*, *T. hirtus*, and *T. orbatus*; species known or suspected to attack *Amegilla* include *T. histrionicus*, *T. picaron*, and *T. ramosus*, whilst *T. truncatus* attacks bees of a different subfamily (Eucerinae). *Thyreus elegans sensu lato* is suspected to attack *Amegilla* (*Micramegilla*) Brooks, 1988 based on co-occurrence (TJW, unpublished data), and hypotheses are presented here for associations between *T. jansseni* and *T. scutellaris* with *Anthophora* (*Mystacanthophora*) species. Even in the absence of a modern phylogeny of the genus *Thyreus*, it is difficult to see how this would translate into a pattern of conserved host use relative to the phylogenetic structure seen in apid bees (Bossert et al. 2019).

Finally, whilst generic concepts are currently under revision in melectine bees due to the generation of powerful new genetic data and morphological analyses (Onuferko et al. 2021; Orr et al. 2024), the present work serves to restate the need to robustly test species-level concepts. It also emphasises the importance of balancing molecular results with morphological criteria. Although genetic variation in the COI barcode is much higher in *T. truncatus* than in other *Thyreus* species studied here, it was not possible to find morphological criteria consistent with barcode clustering to allow for taxon delineation; hence, a conservative and broad species concept was maintained. Whilst the high barcode differences suggest a pattern of historical isolation, perhaps in an Iberian refugium for Iberian specimens, reliance purely on genetic distance would produce a challenging system for morphological identification, as well as potentially lead to nomenclatural instability depending on which mitochondrial lineage the lectotype is assigned to. This approach is consistent with other recent treatments (e.g. Praz and Benon 2023) and will hopefully maintain the fundamentally robust species concepts of Lieftinck (1968) for current and future species monitoring.

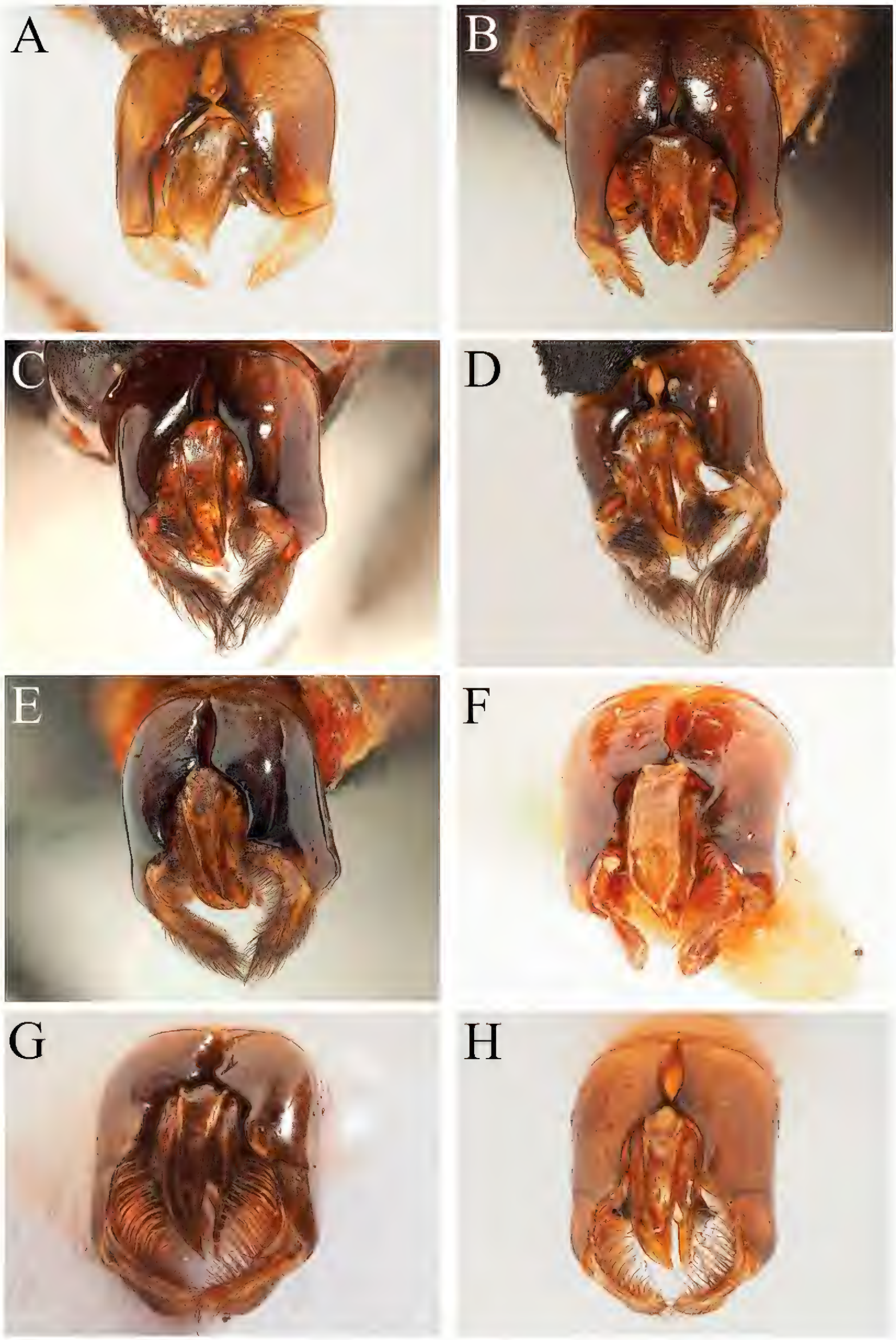

Figure 28. *Thyreus elegans* (Morawitz, 1877) male. **A.** Genital capsule, dorsal view. *Thyreus affinis* (Morawitz, 1873) male; **B.** Genital capsule, dorsal view. *Thyreus hirtus* (Beaumont, 1940) male; **C.** Genital capsule, dorsal view. *Thyreus histrionicus* (Illiger, 1806) male; **D.** Genital capsule, dorsal view. *Thyreus truncatus* (Pérez, 1884) male; **E.** Genital capsule, dorsal view. *Thyreus orbatus* (Lepeletier, 1841) male; **F.** Genital capsule, dorsal view. *Thyreus hohmanni* Schwarz, 1993 male; **G.** Genital capsule, dorsal view. *Thyreus ramosus* (Lepeletier, 1841) male; **H.** Genital capsule, dorsal view.

Figure 29. *Thyreus elegans* (Morawitz, 1877) male. **A.** T1, dorsal view. *Thyreus affinis* (Morawitz, 1873) male; **B.** T1, dorsal view. **C.** Scutellum, dorsal view. *Thyreus hirtus* (Beaumont, 1940) male; **D.** S8, dorsal view; **E.** Lateral part of T1, dorsal view. *Thyreus histrionicus* (Illiger, 1806) male; **F.** Lateral part of T1, dorsal view.

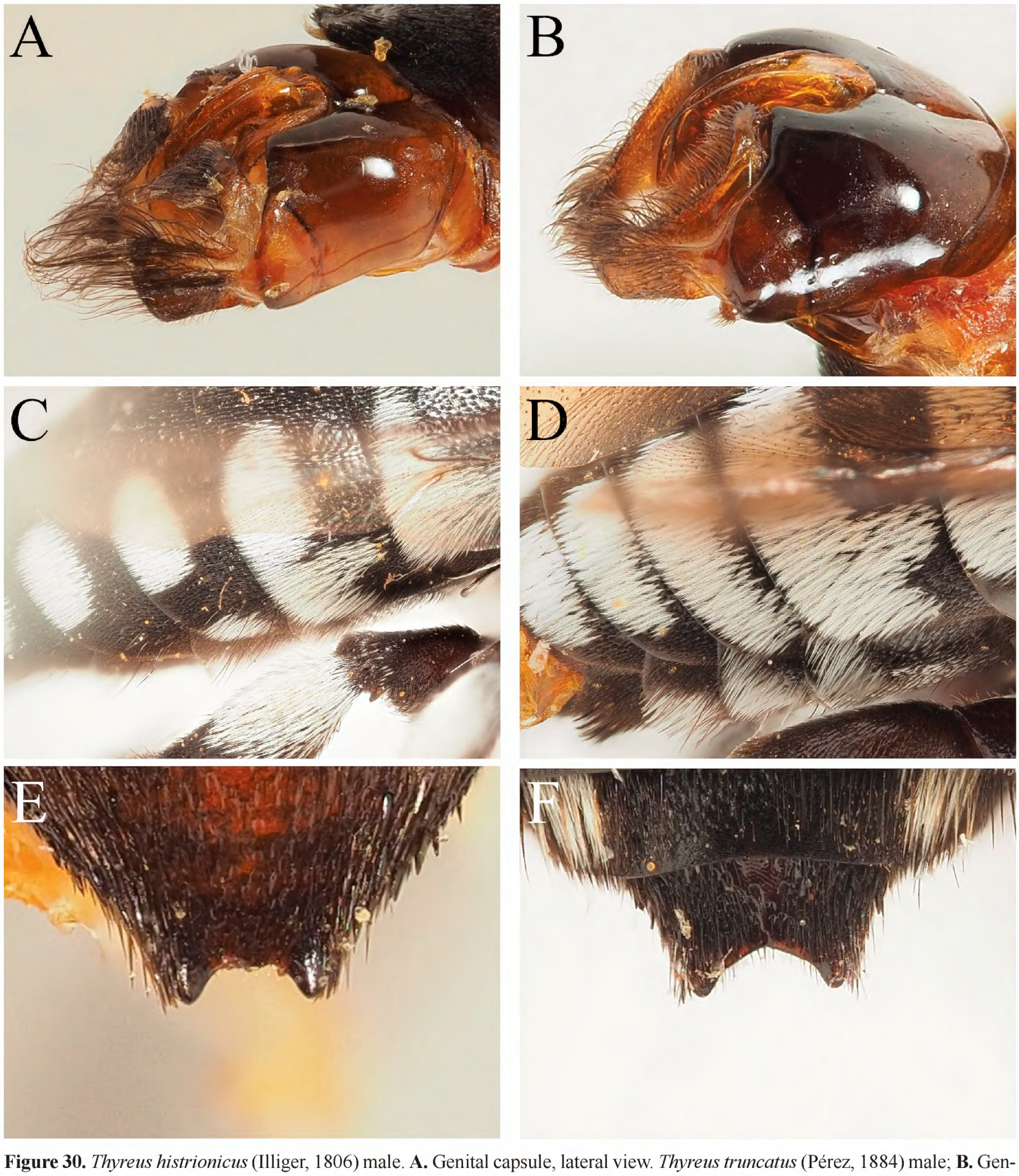

Figure 30. *Thyreus histrionicus* (Illiger, 1806) male. **A.** Genital capsule, lateral view. *Thyreus truncatus* (Pérez, 1884) male; **B.** Genital capsule, lateral view. *Thyreus orbatus* (Lepeletier, 1841) male; **C.** Metasoma, lateral view. *Thyreus ramosus* (Lepeletier, 1841) male; **D.** Metasoma, lateral view; **E.** T7, dorsal view. *Thyreus hohmanni* Schwarz, 1993 male; **F.** T7, dorsal view.

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Supplementary material 1

Additional records of *Thyreus*, *Anthophora*, and *Amegilla* species not detailed in the main text

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Data type: xlsx

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